ENCOURAGEMENTS AND CONSTRAINTS IN THE DEVELOPMENT OF EXPERIMENTAL ANIMAL BEHAVIOUR STUDIES IN GREAT BRITAIN SINCE THE LATE NINETEENTH CENTURY

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ABSTRACT

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Encouragements and constraints in the development of experimental animal behaviour studies in Great Britain since the late nineteenth century

This thesis sets out to identify and explain the encouragements and constraints (both 'internal' academic, and 'external' institutional, political, legislative and social) bearing upon the progress of British scientific studies of animal behaviour between the late nineteenth century, when Great Britain held a dominant position resulting from the influence of Darwinian theories, and the 1970s, when, internationally, animal behaviour studies reflected a wide range of methods and applications. The analysis of these influences is supported by an accompanying consideration of the nature of the work that resulted. Although a focus is held on British contexts, the early loss of the lead in the subject has required an investigation of contrasting conditions encouraging its ensuing development especially in the United States of America, where the favourable institutional and cultural environment helped to explain why its absence in the United Kingdom restricted development there.

The later interactions of laboratory animal psychology and ethology, the continuing role of key figures (a significant proportion of whom in the first quarter of this century were women) including their backgrounds, interests and achievements, together with political attitudes to science, organized professional activity, and the policies of individual academic establishments, bring the study through later decades to the point of further influences, such as that concerning the expansion of the universities, international collaboration in the development of new theories, and the strengthened awareness of ethical cost in experiment.

Original surveys reveal the pattern of output in terms of named investigators, work bases, subject areas and animals used, from the main specialist British journals between 1938 and 1959; the principal investigators of the 1960s, with an assessment of their work; and all known published work undertaken in Britain in the 1970s, including full details of two specimen years, and of the activities of the decade's more productive workers.

To J., D. and K.

CONTENTS

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INTRODUCTION

This work examines the historical development in Britain of the experimental manipulation of captive non-human animals which has been undertaken in order to enable studies or modification of mental processes and behaviour, in the context of either pure or applied research. Activities concerned with detached field observation, or with non-psychological processes, such as purely physiological ones, are not addressed unless they had a direct impact on the progress of the subject under investigation. It is proposed that this historical development, oriented to the period between the 1870s and the end of the 1970s, falls within four phases. These phases are characterized by influences which reflect not just the progress of an evolving subject area but also its changing contexts and circumstances.

The scientific study of animal behaviour had been put on a more secure footing after the publication of Darwin's *The Expression of the Emotions in Man and Animals* in 1872. Darwin's evolutionary theories are usually associated with the explanation of the development of physical characteristics in animals (human and non-human) reflecting the influence of heredity and the environment. During the nineteenth century his demonstration of human kinship with the animal world through the apes provoked controversy. Assumptions about human uniqueness and the religious beliefs that humans were separate and different from the rest of creation were brought into question.

But Darwin's work was significant not just for its attempt to explain the evolution of those physical attributes in animals that made them fit and able to compete and survive in their environments. He also suggested that behaviour had evolved and that in this evolution there were again links between humans and animals.

Meanwhile in the second half of the nineteenth century scientists in Germany had begun to investigate human psychological behaviour more precisely by employing laboratory techniques and instruments to measure performance in memory, discrimination and sensation. Gradually their more practical, research-based approach came to influence British workers, some of whom had studied under them, and the traditional links between 'armchair' psychology and philosophy began to be loosened. Indeed, as a result, many conservative philosophers, as well as some religious commentators, rejected this new psychology as insulting to human dignity, and when, in comparative psychology, similarities were demonstrated between man and animals, much experimental psychology was in this hostile climate able to break away completely to form a new specialist discipline.

With Darwin's ground-breaking theories, and the refinement of experimental methods in Germany, the scene was set in the late nineteenth century for a number of British investigators to begin systematic studies of animal behaviour. Among these was Conwy Lloyd Morgan who carefully observed the efforts of his dog to solve problems like pulling a long stick or bone through vertical iron railings. Lloyd Morgan noticed that a lot of 'trial and error' was involved, and this was a phrase he coined. However, unlike some of his contemporaries who recounted anecdotes of seemingly impressive feats of animal intelligence, he resisted the temptation to attribute too much to the mental ability of an animal. He is remembered for his Canon, which is a variation of a law of parsimony or of Occam's Razor: 'In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of one which stands lower in the psychological scale'.[1]

This objective and critical approach was enthusiastically taken up at the turn of the century by animal psychologists working in America, where society through its educational institutions was more willing than in the UK to support the development of a new science, one that soon became centred on laboratory work. At this time the British lead was lost to the USA, and the Americans became engrossed in learning theory and Behaviourism, based increasingly on immediate observations of outward behaviour in the laboratory rather than on attempts to interpret the significance of evolved mental processes, and less and less on the evolutionary theories of Darwin. This was the time when the white rat became the characteristic laboratory animal of the psychologist who wanted to establish laws for learning and motivation. 'Rat psychology' has never developed as strongly in Britain, but at the same time the promising opportunities presented by Darwin's theories were neglected after the turn of the century in the UK, too, where work in animal psychology was limited for 50 years.

Changes in the level of the British contribution suggest a number of questions. Why did this new and pioneering work decline so quickly in Great Britain? To what extent did it continue after the turn of the century? What influences were exchanged among

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[1] Lloyd Morgan, C. (1894) *Introduction to comparative psychology*. London: Scott.

the UK, USA and continental Europe? How did animal psychology itself evolve and diversify? In the UK, was its development controlled by scientific and academic preferences, or did the economic, legislative, social and institutional contexts in which a subject like this found itself determine the rate of its progress? In which British universities was the research established after the turn of the century and by whom?

Among these interesting questions, which need to be asked of any scientific discipline's historical development, there are some peculiar to this one which require an explanation. Why was it that in the early years of the century, when few in Great Britain were involved in laboratory-based studies of animal behaviour, there was an unusually large number of women engaged in this limited area of work? To what extent did field studies of animal behaviour complement or compete with the laboratory work? What was the nature of relations between comparative psychology and ethology, which began to be established securely in Britain by the mid-twentieth century? Did the potential of comparative and animal psychology as applied sciences encourage the development of the discipline or did this role mean it later became relegated as a secondary research area serving others (such as pharmacology, agriculture or psychiatry)?

While research in applied animal behaviour later revealed workable information on pest control, camouflage, effects of drugs, breeding, neuroses etc., it experienced at first some bizarre failures in other areas. One of these was anti-submarine warfare in the First World War. Such military activities, and many other areas of applied laboratory studies of animal behaviour, have raised another question, that of ethical cost. However, it was not until the 1970s that animal psychology became in the United Kingdom a research area drawing levels of criticism from campaigning groups, moral philosophers, and psychologists themselves, equal to those levelled at other biological sciences involving animal research. Indeed, objections to animal experimentation have focussed since the mid 1970s especially on psychological work. Public opinion has expressed concern about many non-medical research programmes involving animals, and invasive psychological work has come to be placed by it in the same category of allegedly dubious and undesirable research as cosmetics testing. But how much thought, if any, had been given to such ethical matters in animal psychology since the turn of the century? Have pressure groups had any influence on the historic development of animal psychology in the UK?

More recently, it has been argued that if an animal is psychologically like us, there may be more scientific reason to experiment, but less moral justification to do so. In response to this dilemma, some scientists deny it exists: they say that although there are scientifically valuable similarities between humans and animals that make experimentation worthwhile, humans are at the same time unique and fundamentally different. This outlook is, ironically, typical of the pre-Darwinian era. (Another irony is that debate about these issues has facilitated the participation once more of philosophers in questions concerning experimental psychology.) But in this country, certainly more so than in the USA, ethical constraints have prevented the development of psychological research with animals along certain routes, and the professional and academic societies have over the past twenty years published for their members codes of conduct and guidelines that are intended to respond to public concern about the welfare of animals in the psychological laboratory.

By the end of the 1970s the public debate about the perceived value, processes and moral significance of animal behaviour studies had been brought into the open by some vociferous members of the British Psychological Society and by an array of hostile pressure groups, among which the longer-established were turning attention to psychology only for the first time.[2] By 1980 it had also become clear that the 1876 Cruelty to Animals Act, the traditional reference point for discussions on established animal research of all kinds, was to be replaced. Although well regarded by the scientific community, its reform would be the inevitable outcome of protracted public argument, over the decades based largely on the Act's regulation of physiological work. During the 1970s it was also generally agreed that the current Act was inappropriate for much psychological work depending on stimulation, deprivation or motivation rather than on surgical intervention. The introduction of proposals for new legislation and the printed and broadcast debate, lay and specialist, which accompanied it, ensured that by the end of the decade, and for the first time, experimental studies of animal behaviour had become significantly exposed to the external influence of public comment and scrutiny.[3]

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[2]For example, there is no evidence in the British Union for the Abolition of Vivisection archives of any earlier concern for this area of scientific work, and until the Second World War the main objects of criticism were physiology and vaccination.

[3]External influences of this kind are usually denied by those whose work is under threat, and justification and defence of work is reaffirmed internally through the editorials of societies' periodicals, the establishment of codes or the inauguration of specialist groups within societies, such as the Psychobiological Section of the British Psychological Society, which had decided in 1981 not to take out institutional membership of the Research Defence Society. However, signs that organized and sometimes militant opposition was affecting the content and administration of academic research programmes appeared from the 1980s when some prospectuses announced the optional status or absence of animal work, and university departments introduced extra security measures. Bristol University displayed a public notice outside its city centre Department of Psychology in Berkeley Square which announced that animals were not used there.

It is necessary in this historical analysis to adopt both 'externalist' and 'internal' (traditional as well as Kuhnian)[4] approaches, so that the social, political and economic contexts can be assessed together with the internal dynamics of the subject. In these respects, and unless an uncompromising view is taken on one side of the 'nature-nurture' question, it may be appropriate to draw an analogy with the real situation of the animal itself. Its life is influenced, sustained and sometimes threatened by its environment, but at the same time it appears to retain at least some control over the direction of its activities, sometimes with immediate and long-term effects. In the same way, an evolving area of distinct scientific investigation will be conditioned by the changing contexts through which it travels during its development, while those directly and continually involved in its special range of activities will give it a character and momentum of its own. The relationships between a dynamic entity and its operating environment are variable, complex, intimate and often disputed, but an examination of the historical progress of the subject here addressed must nevertheless be based on studies along both of the two research dimensions now associated with the history of science, in order to attempt a more representative understanding.

The adoption of the general method of enquiry outlined above must further be affected by another investigative strategy concerned with the judicious control of temporal and subject-area boundaries. Given that there will be an interaction of themes and chronology, it will be necessary to identify and argue a limited number of key points in time at which changes in development or direction can be proposed. For example, such a point will later be proposed as belonging to the few years after the turn of the century. To understand the nature of the position reached at that time it will be necessary to carry out a formative and summative assessment of the preceeding period by extending the temporal boundaries back, towards the middle of the nineteenth century, so that the importance of the intervening period can be interpreted within a clear time-frame and drawn in at the key point selected. At the same time, movement back in time from this point, by which a significant level of relevant activity was taking place, will involve in this early historical phase an extension of, and lessening of focus on, the subject area boundaries, from those specifically concerned with animal psychology successively back to the related, earlier and contributing areas of science. Through an investigation of external and internal influences, of the establishment of key historical phases and points of change, and of interrelationships with antecedent and concurrent science disciplines, the evolution of the subject will be interpreted and a pattern of encouragements and constraints established. It will become apparent that

[4]Kuhn, T.S. (1962 and 1970) *The structure of scientific revolutions*. Chicago: University Press.

because in the earlier stages of historical development a limited quantity of work was carried out, a closer and more complete qualitative analysis is possible. For the final stage of the study, beginning in the early 1960s, the quantitative interpretation is summarized in the form of trends in representative years because of the great volume and complexity of work undertaken from that time.

The two existing major histories addressing the development of British animal psychology have been written by psychologists who have opted for a traditional 'internal' treatment, and in them the progress of British work since Darwin has been set either in a more extensive historical time-frame, with other areas of psychology integrated into the account,[5] or in a context which serves primarily to explain international progress.[6] The present work retains a British perspective and, within a delimited historic period, concentrates on a specific area of the general discipline of psychology. Secondary sources have been selected to illuminate the professional and more general environments that affected the progress of the subject. These have been tested by reference to a range of primary and archival sources bearing on the development of the subject and its practitioners, and reflecting mainly the institutional context. The importance of analyzing the general or 'external' environment as part of the historiography of psychology began to be emphasized in the 1960s. Young drew attention to the variety of approaches, standards and special interests underlying the historical treatment of the behavioural sciences (a 'nebulously-bounded field'), and noted the arrival in 1965 of the American *Journal of the History of the Behavioral Sciences* as a reflection of the enthusiasm for the historical investigation of this field, but expressed concern at the continuing 'whom to worship?' tendency in historical accounts which were based on the mistaken and uncritical acceptance of secondary sources for primary ones, and criticized the lingering habit of interpreting the past through current perspectives.[7] This habit was also later alluded to by Mackenzie and Mackenzie when they discussed the phenomenon of 'presentism': there had developed a tendency to consider the history of scientific psychology almost as the history of behaviourism, simply because that school had held such sway in recent decades.[8]

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[5]Hearnshaw, L.S. (1964) *A short history of British psychology 1840-1940*. London: Methuen.
[6]Boakes, R.A. (1984) *From Darwin to behaviourism: psychology and the minds of animals*. Cambridge: University Press.
[7]Young, R.M. (1966) Scholarship and the history of the behavioural sciences. *History of Science*, 5: 1-51.
[8]Mackenzie, B.D. and Mackenzie, S.L. (1974) The case for a revised systematic approach to the history of psychology. *Journal of the History of the Behavioral Sciences*, 10.

The preparation of the present work has required a thorough examination and analysis of such secondary sources, involving at first consultation with Information Librarians at the University of Leicester in order to confirm appropriate investigative strategies and to identify suitable procedures to ensure a comprehensive search. A manual search of books and serials included a full inspection of all volumes of *ISIS* (1913 to date), *Psychological Abstracts*, *Behavioural Biology Abstracts* and *Animal Behaviour Absracts*. Use has been made of the University of London Library which holds the former collections of the library of the British Psychological Society. In addition, an on-line search of specialist databases was carried out.[9]

The range of primary source material identified and consulted is revealed in the relevant section of the Bibliography. It consists of archival and manuscript material held in universities and colleges which fulfilled a significant historical role in the development of the work under study; of Government documents in the Public Record Office; of archival sources elswhere which are indicative of public interest and of the activities of monitoring or campaigning organizations; and of correspondence with some of those who have commented on their personal experience of historic events or circumstances.

Most of the published evidence for 80 years' laboratory-based research into animal behaviour in Great Britain from the turn of the century to the 1980s has been brought together in this thesis for the first time, so that relative patterns of activity and interest, based on people, places and research areas, as well as on the general social environment in which this form of science developed, can be accurately identified and discussed. Tabular information in the appendices consists of raw data for the later periods brought together in an original compilation to serve this purpose. Prosopographical accounts are provided for key figures in this development, and attention is drawn where appropriate to those who held positions of influence capable of progressing or retarding specific advances in Great Britain of scientific studies of animal behaviour. The evidence offered is intended primarily to serve the objective of demonstrating that studies of animal behaviour in Great Britain this century have fallen into four distinct historical phases of development. Influential trends and personalities, funding arrangements and a range of external influences are incorporated into the account. The first phase ended before the First World War with the final contributions of L.T.Hobhouse, whereupon a new phase of restricted and often derivative work

[9] *PsycLIT* on CD-ROM; BIDS *UnCover*; BIDS *British Library Inside Information*; BIDS ISI Data Service: *Science Citation Index* and *Social Sciences Citation Index*; OCLC FIRSTSEARCH *WorldCat* and *Article 1st*; LIBERTAS.

lasted until the 1940s. A strengthening and variation of experimental programmes took place after the Second World War, and following this third phase the final period of development from the early 1960s was accelerated as a result of university expansion and new research purposes, opportunities and techniques.

General theoretical developments known to have had a practical effect on research work as significant influences merit attention. The development of theoretical frameworks in Britain itself in the new century was for a long time extremely limited.[10] However, the scientific study of animal behaviour had first been made possible by those original theoretical frameworks contained in Darwin's *The expression of the emotions in man and animals* of 1872,[11] which proposed that the instincts, emotions and intelligence of non-human animals differed from those of man only in degree and not in kind. Darwin himself undertook research on instincts using the Hymenoptera (ants, bees and wasps) to refute teleological views and to show that instincts could evolve through natural selection.[12] It has been noted that he stood at the threshold of a new empirical psychology which was itself encouraged by the example of his own practical investigations.[13] With the notion that the minds (and behaviour) of various species stem from common descent, the grounds for a comparative psychology became greatly solidified. Darwin concluded : 'There is no fundamental difference between man and the higher mammals in their mental faculties.'[14] In *Expression*, Darwin showed, as he had in other works, how careful, comparative observations of behaviour could shed light on important principles of behavioural evolution. The evolution of behavioural patterns could be studied just as could the evolution of structure. Darwin was well aware of the implications for psychology. He wrote, 'Psychology will be securely based on the foundation ... of the necessary acquirement of each mental power and capacity by gradation. Much light will be thrown on the origin of man and his history.'[15] As one result, the anecdotal method in comparative psychology was triggered by Darwinism and by the effort to demonstrate behavioural continuity between humans and nonhuman species. But alongside the anecdotes and the anthropomorphic interpretations that tended to disguise in the published literature

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[10]Hearnshaw, L.S. (1969) Psychology in Great Britain: an introductory historical essay. *Supplement to the Bulletin of the British Psychological Society*, 22: 3-9.
[11]Darwin, C.R. (1872) *The expression of the emotions in man and animals*. London: John Murray.
[12]Angell, J.R. (1909) The influence of Darwin on psychology. *Psychological Review*, 16: 152-69; Ghiselin, M.T. (1973) Darwin and evolutionary psychology. *Science*, 179: 964-8.
[13]Hilgard, E.R. (1960) Psychology after Darwin. In: Tax, S. (ed.) (1960) *Evolution after Darwin*, Vol.II: 269-87. Chicago: University Press.
[14]Darwin, C.R. (1871) *The descent of man and selection inrelation to sex*. London: John Murray, p.446.
[15]Darwin, C.R. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray, p.373.

much of the critical scientific analysis underlying the work of the late nineteenth century investigators, there was plenty of evidence for the development of objective experimental methods to address behavioural questions. For example, to examine the ontogeny of behaviour, noting that white, blue-eyed cats are deaf, Darwin experimented with normal young kittens, which also have blue eyes, and found that these were deaf too. A failure of the developmental mechanism in these cats had led to an imperfect sensory apparatus.[16] 'Darwin foresaw that by analyzing behavior in terms of developmental mechanics, much of psychology could be reduced to physiology. Some changes in behavior are due to inherited modifications in the structure of the nervous system.'[17]

In a comment equally appropriate to the position of comparative psychology, a zoologist later asked why ethology, having arrived at that time an apparently healthy though nameless infant, then had its development arrested for several decades in the following century.[18] Part of the problem, he proposed, was the reluctance of psychologists to accept and act on the full implications of evolution, which would even have allowed some legitimate anthropomorphism. As for zoologists, they concentrated excessively on physiological and anatomical matters and neglected processes, functions and behaviour, a scientific disposition epitomized in the disagreements of Darwin and Richard Owen. 'Darwinism did not constitute a unified research programme, and by the end of the century the fragile unity imposed upon several diverse fields by the appeal to Darwin's name as a figurehead had broken down.'[19] The influential contributions of non-scientific commentators such as Samuel Butler and George Bernard Shaw, both of whom supported Lamarckism as a more humanistic model of evolution and who vigorously and emotionally opposed Darwinian materialism, did not pass without effect, either, on the social environment in which a systematic study of the possibilities presented by Darwinian theories could have been encouraged. Shaw's campaign was long-lasting. He wrote to Julian Huxley in 1942: 'Biology is in a bad way. The Laboratory mind is more degenerative than malaria. The descent from Huxley, Darwin and Spencer - broken by Butler, Bergson and Back to Methuselah - to the simpleton Pavlov is a precipitous *dégringolade*.'[20]

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[16]Darwin, C.R. (1875) *The variation of animals and plants under domestication*. London: John Murray, pp.322-3.
[17]Ghiselin, M.T. (1973) Darwin and evolutionary psychology. *Science*, 179: 964-8.
[18]Pumphrey, R.J. (1952) Ethology comes of age. *The Advancement of Science*, VIII, 32: 374--8.
[19]Bowler, P.J. (1992) *The Fontana history of the environmental sciences*. London: Fontana Press, p.307.
[20]Huxley, J.S. (1970) *Memories*, Vols I and 2. London: George Allen and Unwin Ltd, p.252. (*Dégringolade*: a tumbling down.)

British behavioural work in the last thirty years of the 19th century was, by the standards of the American work in the following century, limited, irregular and sometimes unsystematic. However, during this period, England was the only country in which investigations of animal behaviour were undertaken on a scientific basis. Spalding[21] carried out highly innovative, precise and objective experimental research in order to attempt to distinguish instinct from experience in animal actions, using chicks and piglets. Darwin's friend and neighbour Lubbock[22] investigated especially the behaviour of insects: being a sceptical and thoughtful scientist, he 'understood the need to collect data, but he did not understand that the hypothesis posed by the observer also determines the nature of the questions asked, that the nature of the question should determine the nature of the controls, and that the nature of the controls should determine permissible interpretations.'[23] Nevertheless, Darwin himself claimed that he relied on the opinions of three men only, Hooker, T.H.Huxley and Lubbock, and on the latter's most of all because of the course of his studies and the clarity of his mind. Romanes[24] published accounts of animal behaviour of a largely anecdotal kind, but the rigour of his scientific work has lately been re-assessed,[25] and Darwin had originally bequeathed much of his unpublished writing on animal behaviour to him, some of this material on instinct being incorporated into Romanes's *Mental Evolution in Animals*.[26] 'It was Haeckel ... who described George Romanes as the first to recognize psychology as the ultimate expression of Darwinism, which is what Romanes's *Animal Intelligence* (1881) set out to establish.'[27] In the 1880s Romanes and Conwy Lloyd Morgan engaged in a controversy concerning the possibility of a comparative science of psychology, the definition of instinct, and the automatism doctrine of consciousness:[28] the former two topics have persisted ever

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[21]Spalding, D.A. (1873) Instinct: with original observations on young animals. *Macmillan's Magazine*, 27: 282-93; Haldane, J.B.S. (1954) Introducing Douglas Spalding. *British Journal of Animal Behaviour*, II: 1; Sparks, J. (1982) *The discovery of animal behaviour*. London: Collins.
[22]Lubbock, J.A. (1882) *Ants, bees, and wasps*. New York: Appleton; (1883) *On the senses, instincts and intelligence of animals with special reference to insects*. New York: Appleton.
[23]Candland, D.K. (1993) *Feral children and clever animals. Reflections on human nature*. Oxford: University Press, p.166.
[24]Romanes, G.J. (1878) *Evening discourse delivered before the British Association*, Dublin. London: Taylor & Francis; (1882) *Animal intelligence*. London: Kegan Paul, Trench & Co.; (1883) *Mental evolution in animals*. London: Kegan Paul, Trench & Co.; (1885) *Jelly-fish, star-fish and sea-urchins. Being a research on primitive nervous systems*. London: Kegan Paul, Trench & Co.; Romanes, E.G. (1896) *The life and letters of George John Romanes*. London: Longmans, Green & Co.
[25]Rollin, B.E. (1989) *The unheeded cry: animal consciousness, animal pain and science*. Oxford: University Press.
[26]Gottlieb, G. (1979) Comparative psychology and ethology. In: Hearst, E. (ed.) (1979) *The first century of experimental psychology*. Hillsdale, New Jersey: Lawrence Erlbaum Associates, p.149.
[27]Thompson, R.F. and Robinson, D.N. (1979) Physiological psychology. In: Hearst, E. (ed.) (1979) op. cit., p.421.
[28]Gray, P.H. (1963) The Morgan - Romanes controversy: a contradiction in the history of

since. Lloyd Morgan had intended to become a mining engineer, but during a dinner at the Royal School of Mines, Huxley suggested he might like to work with him, and after further study at the Royal College of Science he became one of Huxley's disciples. He was a strong advocate of an evolutionary approach in comparative psychology and later in retirement set out a doctrine of the emergent evolution of consciousness.[29] Of his many experiments, most were relatively informal studies of animals outside the laboratory in more natural surroundings. While recognizing the limitations of anecdotes, he did use them on occasion. Lloyd Morgan[30] and Hobhouse[31] indeed built on the possibilites presented by Darwin, but became distracted by other commitments or interests (Lloyd Morgan by administration at Bristol, and Hobhouse by sociology and journalism); although Lloyd Morgan continued varied correspondence with workers in every aspect of animal behaviour on his retirement in 1920 to the south coast of England and until his death in 1934.[32] In 1899 Lloyd Morgan had become the first Fellow of the Royal Society to be elected for work in psychology, and in 1921 he was also elected the first president of the psychological section of the British Association.[33] In an examination of 40 histories of animal behaviour studies in which 214 different investigators who were professionally active before 1914 were mentioned in 895 citations, Darwin and Lloyd Morgan were discovered to be most frequently referred to as the founders of the discipline;[34] and Lloyd Morgan above all others established among psychologists the evolutionary point of view in the empirical study of animal behaviour.[35] At the end of the nineteenth

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comparative psychology. *Proceedings of the Montana Academy of Sciences*, 23: 225-30.
[29]Lloyd Morgan, C. (1923) *Emergent evolution*. London: Williams and Norgate.
[30]Lloyd Morgan, C. (1890) *Animal life and intelligence*. London: Arnold; (1894) op. cit.; (1896) *Habit and instinct*. London: Arnold; (1900) *Animal behaviour*. London: Arnold; (1912) *Instinct and experience*. London: Macmillan; (1930) *The animal mind*. London: Arnold.
[31]Hobhouse, L.T. (1901) *Mind in evolution*. London: Macmillan.
[32]Lloyd Morgan's desk became a forum for most of those involved in psychological research with animals in Britain until the 1930s. All types of investigator as well as some foreign workers corresponded with him. New publications were exchanged and admired, and points of disagreement discussed. (Detailed references to the records of the following correspondents in the Bristol University History Collection can be found below under Primary Sources.) Sherrington (1901) writes in appreciation of his newly received copy of *Animal Behaviour*; and much later both he (1923) and, via his wife, an infirm Henry Head (1929) express great interest in Lloyd Morgan's published studies of 'emergent evolution'. Margaret Washburne (1913) refers to Lloyd Morgan's criticisms of her *The Animal Mind*, to her misgivings about Watsonian behaviourism and to her appreciation of Lloyd Morgan's *Instinct and Experience*. Much further correspondence on each other's work took place between Lloyd Morgan and C.S.Myers, E.B.Poulton (Hope Professor of Zoology at Oxford), William McDougall, J.A.Thomson et al. Lloyd Morgan remained at the centre of a network of correspondence on matters concerning animal behaviour long after he ceased his own experiments.
[33]Richards, R.J. (1977) Lloyd Morgan's theory of instinct: from Darwinism to neo-Darwinism. *Journal of the History of the Behavioral Sciences*, 13: 12-32.
[34]Standing, L. and MacLean, M. (1991) Contributions to the history of psychology: LXXVIII. Citation overlap between histories of animal behavior studies. *Psychological Reports*, 68: 707-10.
[35]Hilgard, E.R. (1960) op. cit.

century in the United States of America, general psychology, which at the time was 'primarily based on philosophy and physiology according to the German model, became more biologically oriented as the result of Morgan's efforts.'[36]

The initiative was then lost to the United States, where new rigorous scientific procedures were applied and the questions recently raised in Great Britain were developed, but along lines that drew away from Darwinian influence and which began to respond to the needs of a demanding, and fortuitously symbiotic, institutionalized educational market. There was now in Great Britain and until after the Second World War little development of theory or practice as in the United States, on the Continent and in Russia (representing, respectively, behaviourism, ethology and reflexology). The infrequent laboratory-based experimental psychology in Great Britain, which was usually based on foreign investigations and sometimes undertaken only for teaching purposes, is identified and described below. Work in this period was sporadic and came after a clear break in promising developments which ended with Hobhouse, who stood at the boundary between the first and second phases of the historical development of animal behaviour studies in Great Britain.

At the begining of the twentieth century there was little effort or incentive to continue or resurrect significant enquiries in Great Britain, although slender links with Lloyd Morgan and his work remained in those who succeeded him at Bristol: G.C.Grindley and G.C.Drew. There was also some limited development of British psychological departments and laboratories, but university staff occasionally expressed a sense of resignation at institutional failure to support animal psychology (e.g. Beatrice Edgell, see below), while the most powerful academic psychologists, C.S.Myers and F.C.Bartlett at Cambridge, did little to nurture its prospects.[37] Psychology as a subject in general was struggling for recognition and independence in an environment of academic hostility and conservatism, no doubt affected by lingering philosophical and (to some extent) religious attitudes which were themselves out of sympathy with those Darwinian interpretations that could have been so productive for a British comparative psychology, as opposed to an alternative American one. But the investigators themselves were not necessarily irreligious: for example, Lloyd Morgan and Howard[38]

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[36]Adler, H.E., Adler, L.L. and Tobach, E. (1973) Past, present, and future of comparative psychology. In: Tobach, E., Adler, H.E. and Adler, L.L. (eds) (1973) Comparative psychology at issue. *Annals of the New York Academy of Sciences*, 223: 184-92.

[37]It is however true that Myers maintained some interest in animal work and advised E.M.Smith in her Cambridge experiments (see below). After her marriage to Bartlett she gave up such research and clearly failed to create an enthusiasm for it in her husband.

[38]Howard, H.E. (1923) Letter to C. Lloyd Morgan, 13 May 1923. Bristol University History Collection, DM 128/347.

saw no conflicts in naturalistic interpretations and belief in God; and one of God's ministers, the Rev. F.Aveling, led the Department of Psychology at King's College, London for twenty-two years. Furthermore, by the turn of the century society had itself become irreligious, and so the idea of religion as a factor indirectly stunting the growth of British comparative psychology through a supposed conflict with Darwinian principles must be treated with caution, especially in view of the strong position achieved by then of the concept of scientific naturalism.

The problems caused by the First World War (like those of the Second) helped to make psychological work better understood and valued because of its practical applications, but with little material effect on prospects for comparative psychology. There were for the first time secret applied studies of animal behaviour to serve the war effort, although these were not undertaken in collaboration with academic psychologists. At this time too, C.S.Myers undertook a pioneering but frustrating struggle to get psychological evidence and applied psychology accepted, as a result of his experience as an army medical officer dealing with what became referred to as shell-shock.[39] Meanwhile he helped establish experimental psychology at Cambridge, which soon became the principal source of experimenting psychologists, some of whom left to create new university departments elsewhere in Great Britain.[40] But neither Myers nor his student and successor Bartlett, who had acted as 'caretaker' at Cambridge during Myers's absence at the front during the First World War, did much to encourage animal experimentation programmes there.

After the promise of the work of Darwin, therefore, and the attendant research of Lloyd Morgan (whose interest in animal behaviour had at first been encouraged by T.H.Huxley) and Hobhouse, something of a vacuum existed at the beginning of the twentieth century. But although isolated laboratory work appeared only occasionally in the 40 years before the Second World War, there was nevertheless sustained, associated and competing interest in animal behaviour among field naturalists, sometimes wealthy amateurs or academic zoologists, and their work created the background for the formation of the Institute for the Study of Animal Behaviour, for the subsequent introduction of the methods of continental ethology into Great Britain after the Second World War, and for the more recent developments of behavioural ecology and sociobiology.

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[39] W.H.R.Rivers and W.McDougall spent the war in similar capacities.
[40] Myers left Cambridge in order to develop his new interests in applied industrial psychology. Given his recognition of the relevance of animal studies in academic psychology, it is interesting to speculate on the possibility of his having supported its development at Cambridge, had not the diversions of applied clinical and industrial psychology been created by the occurrence of the war.

For the period extending from the beginning of the twentieth century until the outbreak of the Second World War it is possible to identify almost all of the work done. This is a period in which all the promise of a domestic tradition of comparative psychological studies could have been realized but was not. An attempt has been made to identify all the work and describe key early figures, centres of research, operating encouragements, constraints and contexts, and the first, limited instances of the use of animals in psychological laboratories. Because comparatively little was done over the 40 years concerned, the work which was carried out has been largely forgotten, and from the new third phase of development beginning after the end of the Second World War, in American-influenced, neo-behaviouristic psychology and in ethology, it was also no doubt regarded as irrelevant or of little value. But the evidence of what was completed in these 40 years cannot be ignored if the background against which the later resurgence occurred is to be understood. British laboratory work between 1900 and 1940 in fact had little influence on the post-war shaping of research plans and strategies. There had never been any development of a market for psychology as in the United States of America (where there grew a market for educational purposes), and the general economic setbacks of the 1920s further reduced opportunities for progress in such relatively esoteric and controversial academic subject areas. A full account of British work is possible for the period between c.1900 and c.1940, and at this time, because there was a minimum of cross-fertilization of theory and method between Great Britain and foreign countries, work in Great Britain can conveniently be assessed and studied alone.

The Second World War itself played a significant part in the promotion of studies of animal behaviour, and, as ethology and other, laboratory-based studies developed after its end, a further period of development in the scientific study of animal behaviour can be identified, leading to the beginning of the 1960s when after the Robbins Report[41] there began the final, fourth phase of massive development in the creation of new university departments, the emergence of neuroscience that this facilitated, and the incorporation of highly developed ethological theories and methodologies combining field and laboratory investigation.

The war had enabled students of animal behaviour to advise on a variety of subjects of economic or military importance, such as pest control and camouflage,[42] and after the

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[41] L.C.Robbins (later Baron Robbins of Clare Market) was Chairman of the Committee on Higher Education (1961-4) that was responsible for the major expansion and reforms of British university education in the 1960s.

[42] Hindle, E. (1947) Zoologists in war and peace. *The Advancement of Science*, IV, 15: 179-86.

war's end, the government facilitated permanent research of various kinds by the setting up of new laboratories and establishments (Nature Conservancy, Agriculture and Fisheries Research Council etc.), thus helping to institutionalize general animal behaviour research, based both on experiment and observation, and encompassing much more than comparative psychology, and to create professional posts to serve aspects of it.

In the late 1940s, as 'zoological ethology' became firmly established within the strengthened Association for the Study of Animal Behaviour, laboratory-based research in comparative psychology also found some new impetus resulting from a revival of interests in neo-behaviourist ideas from the United States (which had long become the indirect source for Britain of Pavlovian methods). Some sharp disagreement, essentially the nature-nurture controversy,[43] occurred in the 1940s and 1950s between those on the one hand who espoused the ethological approach, requiring some subjectivity in research, and those on the other who rejected attributions of inherited, instinctive and insightful behaviour in favour of objective experiment leading to support solely for environmental influences on learning behaviour, and to reductionist interpretations of animal behaviour.
But 'zoological ethology' and laboratory-based 'comparative psychology' were soon found in this third historical phase to be inadequate descriptions of but two sorts of approach to animal behaviour studies. Indeed, concentration in the laboratory on the Norway rat had produced an experimental psychology which could no longer convincingly be described as comparative. Exchanges of ideas and methods took place: the ethologists gave fuller recognition to the precision, measurement and quantification possible only in the laboratory, while the laboratory psychologists acknowledged the need to be familiar with evidence gathered from careful observation of less controlled, natural behaviour in the field.

Suspicion gave way to reconciliation during the 1950s, and in order for this to happen much debate had taken place, stimulating within professional organizations and their journals new thoughts and arguments which helped to raise the profile of the general study of animal behaviour as more joined in. Meanwhile, and following the tradition set by Julian Huxley in the 1930s, aspects of field research were brought increasingly into the public eye from the 1950s onwards, assisted by the advent of television to

[43] It was Francis Galton who coined the phrase 'nature versus nurture' during his examination of the relative influences of heredity and environment on behavioural attributes.

many homes and by the popularizing work of individuals such as James Fisher[44] and Desmond Morris.[45]

The vigour of debate of the post-war years as well as the recently proven economic importance of animal behaviour studies inevitably helped to create for animal behaviour research a better scientific and professional base from which to diversify and specialize. The Experimental Psychology Group was formed in 1946, and British contributions to domestic and foreign journals increased. At this time, too, laboratory-based studies of animal behaviour began to serve other disciplines such as pharmacology and psychiatry, thereby acquiring further professional, economic and social importance as an activity carried out not just for the sake of its own interest, or without the requirement for results which were intended to be applied in society. Scientists with a wide range of backgrounds now in this third phase became more accustomed to incorporate animal behavioural work in their specialist investigations. Meanwhile significant developments were also taking place in neuro-physiology, which would help illuminate the observations of ethologists and psychologists.[46]

The period between the end of the Second World War and the 1960s witnessed greater foreign influence and professionalization, and a considerable expansion in the output of research. The account given in this study is therefore not as detailed or personalized as that for the pre-war period, but because the greater output was matched by new key research areas, centres of research and scientific journals, it is possible to give a representative analysis of work in animal behaviour in Great Britain between 1940 and 1960, based on articles published during that time in the six key journals. Patterns of activity are revealed which link individual workers, work bases, research subjects, animals used, and scientific journals used to publish papers. The work of the more important scientists and of the professional associations is also discussed, together with the general societal, political and economic contexts in which it was carried out.

By 1960 the study of animal behaviour in Britain was still frequently absent from psychology and zoology courses and was not yet well established as a regular research subject within the universities. At that time there were university psychology departments wanting to provide the necesssary facilities but still deterred by the cost of special buildings and staffing for animal laboratories and by the competition of others

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[44] Hinde, R.A. (1971) Obituary: James Fisher. *Animal Behaviour*, 19: 416.
[45] e.g. Morris, D. (1958) *The story of Congo*. London Batsford.
[46] Thorpe, W.H. (1953) Editorial. *British Journal of Animal Behaviour*, I, 1: 3-4.

for scarce funds. The work of existing animal laboratories was meanwhile only irregularly assisted by government grants, research foundations and other private or semi-private bodies.[47] With its practical worth nevertheless well recognized and public interest in behavioural topics stimulated, the climate was therefore benign when the recommendations of Robbins's Committee led in the early 1960s to a rapid development of higher education. Consequently, in this fourth phase, research into animal behaviour, especially of the laboratory-based kind, was able to take advantage of the opportunity to expand into new university departments and new research areas. The study of animal behaviour was more than ever before spread across the boundaries of academic disciplines, and this sometimes increased the size, role and status of the psychology department, as in the case of the University of Sussex. However, the number of undergraduates involved in these developments remained small and animal behaviour studies continued to grow mainly as a subject for graduate research.[48]

Behavioural experimentation now increased as a tool for research in medicine, genetics, toxicology, nutrition, pharmacology, and many other areas. In the 1960s and 1970s, the validity and survival of comparative psychology as a truly independent research area was therefore often questioned, as at the same time investigators from other disciplines such as physiology and biochemistry influenced the course of behavioural studies in the laboratory and helped to create neuroscience. Laboratory work itself was more and more intended as behavioural research with practical applications of a medical or commercial kind, and the new Research Councils and industry guaranteed a regular demand for results. The study of animal behaviour for its own sake was now found largely among those who had retained the same interest in field studies as the early ethologists. But in the 1960s and after, ethology also further developed its own use of laboratory-based evidence on, for example, hormones and neural mechanisms. Behavioural ecology complemented ethological work and similarly drew on field and laboratory studies; and some more recent sociobiological theories were based on early work carried out in controlled conditions in Britain. In the 1970s international recognition was given to studies in animal behaviour through the award of the Nobel prize for medicine and physiology to Tinbergen, von Frisch and Lorenz. The publication in 1975 of E.O.Wilson's *Sociobiology* represented another landmark for the subject area and another indication that the 1970s were a decade of special

[47]Broadhurst, P.L. and Martin, I. (1961b) The study of higher nervous activity in Britain. *Activitas Nervosa Superior*, 3: 164-76.

[48]Furthermore, legislation did not allow for the licensing of invasive laboratory work for teaching purposes.

historical significance with clear developmental links with the 1960s. The British work of Hamilton on the genetic basis of social behaviour had had a significant influence on Wilson's theories.[49] By the late 1970s, external public participation in certain ethical aspects of research activities in the subject area had also become established permanently and for the first time, sometimes encouraged from within the area itself.

This fourth and final period, extending from the 1960s to the beginning of the 1980s, is therefore characterized by distinct historical features apart from the most spectacular expansion in research, facilities for it and in subject areas investigated at an international level. The same system of analysis as for the previous period is used in this study, but for the first decade the output of British centres of research and the work of the more productive scientists are given closer attention. A particularly thorough and accurate survey of British work in the 1970s has been made possible by reference to *Behavioural Biology Abstracts* and *Animal Behaviour Abstracts*.[50] If in the period between 1900 and 1940 Britain's isolation made a study only of domestic work convenient, the sheer volume of international output that built up after the Second World War has made it necessary to restrict the analysis to the United Kingdom and its waters. Work carried out in Britain by foreign nationals has been included, but not work undertaken by Britons abroad. Although the analysis is therefore geographically restricted, this has been a practical necessity; and it has not prevented appropriate reference to foreign influences affecting British work.

The present study demonstrates that the major theoretical developments in Britain of the second half of the nineteenth century led at first to empirical studies of animal behaviour which were equally innovative and significant. In the transference of the bulk of the research work from the UK to the USA at the turn of the century, British influences consisted at first rather in early contributions to the development of experimental rigour and procedure than in a development of nineteenth century Darwinian theories. The circumstances of this transference are elucidated and were due mainly to certain external conditions characteristic of each nation and reflecting the first historical phase that led up to the first years of the new century. It is perhaps less significant that comparative psychology failed to develop in the UK after Hobhouse than that it succeeded to in the USA, where the new science was employed to serve objectivist theories favoured by what was essentially a new, cosmopolitan,

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[49]Hamilton, W.D. (1964) The genetical evolution of social behaviour, I, II. *Journal of Theoretical Biology*, 7: 1-52.
[50]Bateson, P.P.G. et al. (eds) (1973) *Behavioural Biology Abstracts*; (1974-1980) *Animal Behaviour Abstracts*. London: Information Retrieval Ltd.

more materialistic society willing to consider scientific contributions to social development and control, as within establishment educational provision. The same acceptance of experimental behaviour theory to serve societal objectives was also soon demonstrated by the official support given by the Soviet regime to Pavlov's work after the Russian revolution. The various external environments for animal psychology in the historical phases after the turn of the century therefore had great significance. Meanwhile work in Germany became in the new century rather fragmented, and in France a tendency to remain with Lamarckian theory rather than to espouse Darwinism, meant that in these nations, where there was also the disadvantage of a language barrier (but no greater than that in Russia), studies of animal behaviour did not at first share in Anglo-American developments, only later in the case of the Germanic nations to contribute with continental ethology.
Between the 1900s and 1940, limited British work became subject to two main influences: the extent to which this and other sciences, both in pure and applied form, received encouragement and support from the government and the educational establishment; and the level and effect of foreign, primarily American, influences on 'internal' development. It is clear that in this second phase, British workers were few in number (some having emigrated or abandoned the subject), fared poorly in competition for institutional resources for science, and made many fewer original contributions to their area than had their nineteenth century forebears. At this time parallel influences began to be imported, representing the objectivist methodologies of the USA on the one hand and continental ethology on the other. The effect of these influences was strong, and significant original work in the UK was centred largely on Julian Huxley and E.S.Russell, who helped pave the way for acceptance of ethology and the biologicization of animal behaviour studies. The growth in higher education in this second historic phase nevertheless enabled academic psychology to secure its position in the university curriculum, and new psychology departments and experimental programmes slowly appeared, to become the basis for later expansion. As a new experimental subject it is proposed that animal psychology represented an opportunity for women in the first twenty years of the century to make further inroads into academic science, and the proportion of them engaged in animal psychology was then unusually high. At the same time the disruption of the First World War drew attention to the possibilities of applied psychology, although applied animal work did not benefit from any input from comparative psychologists and was secret until long after the war's end.

The third, post-war phase, leading to the early 1960s and the expansion of the universities following the Robbins Report, is clearly identifiable and delimited by three occurrences. The first of these was the rapid employment of studies of animal behaviour to serve as an applied science (or, sometimes, as no more than a technique) within other, primary research strategies or disciplines, occasionally now in a commercial environment. Secondly, the arrival and acceptance of ethology, as either a complementary or a rival method of behavioural research, was made fully visible and incorporated through Tinbergen into mainstream British academic life. The final characteristic of this third historic phase in the development of animal behaviour studies in Great Britain was the growth in the numbers of academic societies reflecting the expanding range of interests and specializations: the result was an improvement in publication and communication, and therefore a stimulus to further research, and greater possibilities for developing academic, professional and public identities.

CHAPTER 1

SCIENTIFIC AND SOCIAL CONTEXTS IN THE LATE NINETEENTH AND EARLY TWENTIETH CENTURIES

The close scientific environment

The development of the scientific and academic contexts in which opportunities for institutionalized experimental animal psychology could first be realized (even if they were not immediately acted on in Great Britain) was attributable to a limited number of leading figures whose influence varied in extent both at home and abroad and whose significance in some cases has only recently been recognized and properly understood. The perceived role of such figures and the assessment of their activities in relation to the progress of the subject represent the traditional matter of an 'internal' approach to its historical development.

The first British investigator to employ rigorous experimental techniques to elucidate animal behaviour was Douglas Spalding, a Scottish slater who became interested in Darwinian implications of mental continuity between animals and man. He set out to examine the relationship between instinct and the environment as factors affecting the behaviour of neonate animals such as chicks and piglets. After attending free lectures in philosophy at the University of Aberdeen where he heard Alexander Bain talk on the theories of instinct, he left for London to teach and to earn funds for training for the Bar. There he met John Stuart Mill who, discovering in him parallel interest in the scientific value of the experimental approach,[1] introduced him to the political and religious radicals, Lord and Lady Amberley. They employed him as a tutor, and encouraged his animal work in their home in the Wye Valley. In a short series of precise experiments conducted in the early 1870s, he established the existence of inborn or instinctive behaviour (which he believed needed to be practised within a critical period if it were to be effected); the phenomenon of what later became known as imprinting (in the case of the chick, refined by innate recognition of the voice of the hen); and the fact that this too would only be effected within critical periods. His experiments were not carried out in any laboratory, but his careful measures to cause temporary sensory deprivation in his subjects until several hours after birth provided

[1] In 1842 Mill had proclaimed the possibility of a science of mind based on 'observation and experiment', which was then inaugurated only in Germany (*A System of Logic*, 1843. London: Longman, book 6, iii: 2).

convincing scientific evidence.[2] Indeed, like the later ethologists, he believed it important to study animals in as natural conditions as possible in order to achieve reliable results. He died in 1877 as a result of tuberculosis and after his own enthusiasm for work had been destroyed by fatal illnesses among the Amberleys. His intimate relationship with Lady Amberley (who also acted as his assistant), condoned within that unconventional household, as well as his social position and outlook, led to his ostracization and then later the neglect of his discoveries.[3] The result was that 'with psychology's increasing preoccupation with the nature of learning, in the twentieth century his findings were forgotten and had to be rediscovered; and his legacy, that of providing a starting point for an experimental approach to animal psychology, benefited the study of learned, and not innate, behaviour'.[4] His own view had been that instinct and learning were closely linked, instinct guiding learning rather than suppressing it.[5] He also developed materialist interpretations of behaviour, leading to a belief in conscious automatism: such a materialistic psychology did not catch hold in England, but helped to prepare the ground for Watson's behaviourism in the new century.[6]

The unscientific and anthropomorphic observations of the Victorian anecdotalists, by association with whom Romanes's reputation has since especially suffered,[7] had led to Lloyd Morgan's wish 'to get down to bed-rock in the "pure" science of psychology'.[8]

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[2]Until his 1873 paper in the liberal, philosophical *Macmillan's Magazine* (vol. 27, pp. 282-93), entitled 'Instinct; with original observations on young animals', was republished in 1954 (Haldane, J.B.S., 'Introducing Douglas Spalding', *British Journal of Animal Behaviour*, 2: 1-11), he was relatively unknown to modern workers. His first major talk was delivered before the British Association meeting at Brighton on 19 August 1872 and a summary was reprinted in *Nature* (vol. 6) for 10 October under the title 'On instinct', with an enlarged paper in 1873. Spalding's life was short, and his remaining few papers and reviews were almost entirely published in *Nature* between 1873 and 1875.

[3]Untrained as a scientist, he was also shunned by the great scientific institutions like the Royal Society. If the patronage of the Amberleys had not been lost, he might have been able to establish for himself recognition as the founder of the experimental science of animal behaviour.

[4]Boakes, R.A. (1984) *From Darwin to behaviourism: psychology and the minds of animals*. Cambridge: University Press, p.16.

[5]Gray, P.H. (1967) Spalding and his Influence on Research in Developmental Behaviour. *Journal for the History of the Behavioral Sciences*, 3: 168-79.

[6]Gray, P.H. (1968) Prerequisite to an analysis of behaviorism: the conscious automaton theory from Spalding to William James. *Journal of the History of the Behavioral Sciences*, 4: 365-76.

[7]Dewsbury, D.A. (1984) *Comparative psychology in the twentieth century*. Stroudsburg, Pennsylvania: Hutchinson Ross, p.39. 'Romanes laid down three principles to guide his selection [of anecdotes]: alleged facts should be (1) from some authority; (2) observable unmistakably; or (3) corroborated by similar observations ... Regrettably, Romanes's application of his three principles was insufficient, and he is generally written of unfavorably because of his reliance on the anecdotal method. That Romanes was well aware of the principles of the scientific method, however, is demonstrated in his *Jelly-fish, Star-fish, and Sea-urchins* (1885). Such methods were not generally useful in the study of mental continuity in 1882, however.'

[8]Hearnshaw, L.S. (1964) *A short history of British psychology 1840-1940*. London: Methuen, p.100;

'Problems will have to be settled not by any number of anecdotes, but by carefully conducted experimental observations, carried out as far as possible under nicely controlled conditions.'[9] He stressed the need for the precise operational definition of terms and for the replication of experiments, and later asked:[10] 'Did one get out of the animal mind aught else than that which one put into it?'.[11] According to Warden, he began to believe that animal behaviour should be studied for its own sake rather than to influence arguments over mental continuity in evolution,[12] but this interpretation has since been contested. Notwithstanding Spalding's contribution, he has been described as the real founder of experimental animal psychology,[13] and his Canon, later to be relentlessly applied by the Behaviourists, required the judicious application of a law of parsimony in experiment and observation: 'In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of one which stands lower in the psychological scale.'[14]

Lloyd Morgan, C. (1930) *The animal mind.* London: Arnold, pp.263-4.

[9]Lloyd Morgan, C. (1894) *Introduction to comparative psychology.* London: Scott, p.359.

[10]Lloyd Morgan, C. (1930) op. cit., p.248.

[11]Singer, B. (1981) History of animal behaviour. In: MacFarland, D. (1981) *Oxford companion to animal behaviour.* Oxford: University Press; and Gray, P.H. (1963) The Morgan - Romanes controversy: a contradiction in the history of comparative psychology. *Proceedings of the Montana Academy of Sciences,* 23: 225-30. Romanes's research in animal behaviour was concerned with the behaviour of the white-throated capuchin or cebus monkey (*Cebus capusinus*), the chimpanzee (*Pan*), homing of bees, olfaction in crabs (Brachyura), and direction-finding in cats (Felidae), among other topics. Unfortunately he also wrote some popular material, chiefly his *Animal intelligence* (1882), in which he was sometimes uncritical and free in his interpretations, perhaps for commercial reasons and to encourage popular consumption, and because of this he has never received the credit he deserves for his other researches. Lloyd Morgan was a friend and admirer of Romanes but criticized his poor methodology and even that of Spalding. How do we know, he asked, that Spalding's chicks would not move towards any sound? How do we know that his proteges had a specific fear of sparrow-hawks and not a response to unusual noises and objects? Although Lloyd Morgan's own research was not large, he carried out valuable experiments on instinctive behaviour with incubated chicks, ducklings (Anatinae), and other birds. In addition, he examined the roles of imitation and of learning in animal behaviour. Much of our present-day terminology appears to have originated from his writings, and even 'behaviour' and the extensive use of 'animal behaviour' for this area of research can be ascribed to him. That chicks learned by means of trial and error, that successful responses were 'reinforced' and unsuccesful ones were 'inhibited' were all terms that he employed.

[12]Warden, C.J. (1927) The historical development of comparative psychology. *Psychological Review,* XXXIV: 135-68.

[13]Thorpe, W.H. (1956) Some implications of the study of animal behaviour. *The Advancement of Science,* XIII, 50: 42-55.

[14]Lloyd Morgan, C. (1894) op. cit., p.53. A good example of Lloyd Morgan's identification of misinterpretation is quoted by L.T. Hobhouse (1915 *Mind in evolution,* 2nd ed., London: Macmillan, p.298). 'A well-known writer, Dr Andrew Wilson, describes the case of a dog which used to hunt a rabbit nearly every morning down a curved shrubbery, and each time ran it into a drain at the end. "The dog then appears to have come to the conclusion" - I quote Dr Wilson's words - "that the chord of a circle is shorter than its arc, for ... he took the short cut ... was ready ... and caught him."' Wilson himself specialized in popular accounts of natural science topics. In the preface of his *Studies in life and sense* (1887 London: Chatto & Windus) he wrote: 'The essays included in this volume have appeared from time to time in various magazines ... The sole aim of the Essays now collected will be fulfilled if they succeed in explaining, to those "willing to know," some of the great facts and laws

This approach has been explained as a measured attempt to reinforce the special status of man:

> As we look back now at the typical Enlightenment view that was so confidently expressed by Lloyd Morgan ..., what we see is surely a rigorous, deliberate widening of the gap between humans and all other animals. It was an antiseptic attempt to protect the human race from pollution by cutting its links with the rest of nature ... Notions about the species barrier slipped right back from Darwin's emphasis on continuity towards something very close to Descartes' position, regarding non-human animals as simple, unconscious machines,[15]

a position soon to be adapted by the behaviourists who took over from Lloyd Morgan. However, Rollin denies that Lloyd Morgan was responsible for the use to which his ideas were put by Watson and other behaviourists,[16] and influential British psychologists who belonged to the generation succeeding Lloyd Morgan's remained sceptical about the value of behaviourism (for example, C.S.Myers in his presidential address to Section J of the British Association in 1931).[17] In fact, and unlike his former mentor, T.H.Huxley, Lloyd Morgan soon rejected Cartesian aspects of neo-Darwinism and the theory of conscious automatism, as being incompatible with an

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which underlie the every-day life both of man and his lower neighbours - animals and plants alike. There are many less effective things, in the way of modern culture, than a popular training in biology'.

[15]Midgley, M. (1994) Bridge-building at last. In: Manning, A. and Serpell, J. (eds) (1994) *Animals and human society - changing perspectives*. London and New York: Routledge, pp.189 & 192.

[16]Rollin, B.E. (1989) *The unheeded cry: animal consciousness, animal pain and science*. Oxford: University Press, pp.75-8. He states: 'The fundamental, crucial arguments against seeing Morgan's Canon as a refutation of the Darwin-Romanes view of the continuity of mentation and, consequently, as a denial of consciousness to animals are two: first, that it was not so intended by Morgan; and, second, that even if it were so intended, far from denying animal mentation, it in fact presupposes it, in order even to make sense ... Then why the Canon? Simply because, in Morgan's view, other comparative psychologists have been too quick to attribute *reason* to lower animals. Contrary to the traditional division of mental intellectual faculties into instinct and reason, Morgan advocates a tripartite division into instinct, intelligence and reason ...'.

[17](*Reports*, pp.185-6; 194) '... the "behaviourists" are quite right when they insist that scientific measurement is applicable only to the behaviour of the organism. Where they are quite wrong is in their assumption that conscious processes must necessarily be ousted from scientific psychology, because measurement is excluded; the truth being that, even when measurement is excluded, the possibilities of systematic observation and experiment still remain. Natural science surely has a function wider than that of merely reducing its subject-matter to units of space and time. Highly valuable and deserving of the utmost encouragement as is the measurement of behaviouristic data, however helpful be the light they may ultimately throw on mental processes and their general characters, however wider be mental processes than the range of mere conscious experience, the scientific study of the mind by direct observation and experiment is never to be discountenanced or discarded ... The fundamental purpose of consciousness is to enable the self to preserve the organism by guidance and direction, - by the formation and satisfaction of ends and values. As in the evolution of living species something far more is involved than the mere blind running down-hill of a wound-up mechanism ...'

understanding of natural selection. Instead, a reconciliation with evolutionary theory was proposed through 'organic selection', by which an organism was credited with an intentional relationship with its environment.

Not only was Lloyd Morgan's Canon misused or at least misunderstood by some of his American contemporaries, but it also signified for him a cautious willingness ultimately to accept, like Romanes, the possibility of mental evolution and of comparative psychology as a viable subject, notwithstanding his concern for the limitations of language and ejective cognition. The Canon was less an instrument with which to attack Romanes and anthropomorphism (as distinct from anthropocentrism and anecdotes) than evidence that Lloyd Morgan had changed from his earlier view that a science of comparative psychology was not possible, towards a new one accepting it, but with the working precautions contained in the Canon itself.[18]

Lloyd Morgan was flexible enough to believe in three levels of animal mind: percipient, perceptive and reflective, associated with the subconscious, conscious and self-conscious states, for which the latter had a capacity for fore-planning (later 'insightful') behaviour. He therefore soon felt it necessary to elaborate on his Canon, and because of its too literal application in some quarters: 'To this it may be added - lest the range of the principle be misunderstood - that the canon by no means excludes the interpretation of a particular act as the outcome of the higher mental processes if we already have independent evidence of their occurrence in the agent.'[19] Darwin had supplied a strong incentive to carry out comparative work,[20] but, until attention was given it by Spalding, Lubbock[21] and Lloyd Morgan, such work was often spoilt by the intrusion of uncontrolled anthropomorphism. Romanes did use the experimental

[18]Costall has gone so far as to claim that 'the Canon was to provide the ground rules for interpreting animal behaviour *anthropomorphically*.' Costall, A. (1993) How Lloyd Morgan's Canon backfired. *Journal of the History of the Behavioral Sciences*, 29: 113-22.
[19]Lloyd Morgan, C. (1900) *Animal behaviour*. London: Arnold. Dewsbury (1984, op. cit., p.188) notes that the canon has often been misinterpreted. It was not written in an effort to eliminate the attribution of consciousness to nonhuman animals but rather to counteract casual anthropomorphism in comparative psychology. Since its enunciation many scientists have acknowledged that rampant application of it can lead to a denial of the existence of complex processes where complex processes exist. Lloyd Morgan himself found this problem in Thorndike's puzzle-box experiments with cats.
[20]Like Lubbock, Darwin himself undertook experimental studies of small creatures at his home. In the late 1870s he carried on sensory investigations using a variety of improvised stimuli which led to *The Formation of Vegetable Mould, Through the Action of Worms, With Observations on their Habits* in 1881.
[21]Lubbock has been given the credit for being the first to use a maze as a device for the study of learning by animals, the first to use the 'Dressur' training method for testing sensory discrimination, a method later re-invented by von Frisch, and the first to identify the effect of the direction of light source on the movement of ants. Pumphrey, R.J. (1958) The forgotten man - Sir John Lubbock, FRS. *Notes and Records of the Royal Society of London*, 13: 49-58.

method, for example to search for evidence of the inheritance of acquired characteristics: he introduced mutilations and physiological changes in guinea-pig parents, but found no clear evidence that the progeny inherited these changes.[22] Lubbock's study of insects made proper use of laboratory methods in physiological psychology,[23] usually applied in his home, which took advantage of his friendship with prominent physicists and engineers who designed sophisticated experimental apparatus. His guests included Francis Galton who provided psychometric equipment and a whistle with which to examine the sensory physiology of the insects.

Lloyd Morgan had written of the need to establish a research institute for the study of comparative psychology,[24] and he undertook observations under controlled conditions of the behaviour of animals in their normal environment, but as the nineteenth century drew to a close, he lost faith in the ability of animal work to throw light on the human mind. He had come to reject the Lamarckian theory of the inheritance of acquired characteristics and asserted that evolution had been 'transferred from the organism to the environment':[25] animals learn by imitation, and successive generations create from this activity a behavioural tradition, gradually modifiable as the environment might dictate.

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[22]Richards, R.J. (1977) Lloyd Morgan's theory of instinct: from Darwinism to neo-Darwinism. *Journal of the History of the Behavioral Sciences*, 13: 12-32.

[23]Warden, C.J. (1928) The development of modern comparative psychology. *Quarterly Review of Biology*, III, 4: 486-522. Warden called Lubbock the founder of the modern laboratory method of approach. Dewsbury (1984, op. cit., pp.41-2) observes: 'He is credited with originating the use of mazes in the study of learning, with first using puzzle devices and the problem method under laboratory conditions, and with inventing a glass-covered ant nest that permitted long-term observation. Lubbock also used a "preference method", later criticized by Loeb, in studying the sensory capacities of insects. Lubbock (1882, *Ants, bees, and wasps*. New York: Appleton, p.247) wrote, "In order to test their intelligence, it has always seemed to me that there was no better way than to ascertain some object which they would clearly desire, and then to interpose some obstacle which a little ingenuity would enable them to overcome". Such has been the rationale for an enormous number of studies in the last hundred years.' B. Singer (1981, History of animal behaviour. In MacFarland, D., 1981, *Oxford companion to animal behaviour. Oxford: University Press*) adds: '... he shared a friendship and correspondence with Francis Galton, who designed some of his apparatus for him. Although Lubbock had relatively little direct influence on British research, his contribution to work in the United States was much greater, and his pioneer laboratory methods of research on insect behaviour were much appreciated by those seeking experimental techniques. His book *Ants, bees and wasps* (1882), based on years of research, was keenly studied. Some of his original methods, such as maze learning and problem solving in the laboratory, were rapidly adopted as standard techniques. Communication between ants and insect colour vision were among his research interests, and his book on intelligence and the senses of animals (1888) dealt with sensation and instinct both in insects and in the dog. The use of statistical methods, and the care with which he used the reports of others, gave his work an objectivity which was influential on later research.'

[24]Boakes, R.A. (1984) op. cit., p.49. Lloyd Morgan wrote that every piece of comparative and genetic work should be so planned as to contribute something to the establishment or the support of the principles of psychology.

[25]Boakes, R.A. (1984) op. cit., p.50.

The experimental work described in Lloyd Morgan's *Habit and instinct* (1896) illustrated his theory of imitation and also approached the problem of habit formation and learning in birds by 'trial-and-error' (one of the expressions, including 'reinforcement' and 'inhibition', which he coined; and he was largely responsible for giving the term 'behaviour' a central place in psychology). His studies were an important contribution in the application of laboratory methods to the behaviour of higher vertebrates. This work was explained in Lloyd Morgan's Lowell Lectures in the spring of 1896 at Harvard University and in a further series of lectures at other places in the United States of America shortly afterwards. These lectures have been credited with triggering the outburst of American work that followed.[26] Kline began similar work on the chick at Clark University in 1897, and Small introduced the rat-maze there in 1899, but already by the autumn of 1896 Thorndike had begun his work on instinct and habit formation in the chick at Harvard.

The strong influence of British theory as evolved by this time and the sudden American capture of the lead in the new work that resulted from it are represented in the pioneering experiments of Thorndike. Lloyd Morgan's lectures directly influenced Thorndike in his initiation of animal experimentation, and also led him to form his 'connectionist' theory, which he later retained in the face of behaviourism.[27] He set out to develop the theories of Lloyd Morgan by subjecting them to systematic laboratory experiments that would yield quantitative results, and he thereby changed the standards for studies of animal behaviour.[28] However, it has been claimed that 'The history of our work on the problem of instrumental learning in the years since Morgan might well be characterized as a systematic and determined but unsuccessful effort to find an acceptable alternative to Morgan's view.'[29]

> Through his efforts conceptual form was given to instinct, so that it became more amenable to empirical, scientific investigation. Morgan's construction of the concept was ... an evolutionary achievement - his theory underwent gradual transformation from an orthodox Darwinian to a neo-Darwinian formulation. The fate of Morgan's theory of instinct was not a particularly happy one in the years after the publication of *Instinct and Experience*. In subsequent works Morgan turned to more metaphysical explorations of the theory of evolution. The discussion of instinct in Anglo-American countries through the

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[26]Warden, C.J. (1928) op. cit., p.500.
[27]Mackenzie, B.D. (1977) *Behaviourism and the limits of scientific method*. London: Routledge & Kegan Paul.
[28]Boakes, R.A. (1984) op. cit., p.181.
[29]Bitterman, M.E. (1969) C.Lloyd Morgan and the theory of instrumental learning. *American Journal of Psychology*, 82, 1: 126-33.

> 1920s and 1930s became snagged by the provocative neo-Lamarckian views of William McDougall. The behaviorist reaction to what appeared to be violations of the principles of parsimony and empirical verifiability by McDougall (and others of like mind) turned attention away from instinct theory in English-speaking countries for several decades.[30]

This occurrence marked the loss of the initiative in Great Britain in the experimental study of animal behaviour, and its great significance for animal behaviour studies here and elsewhere deserves careful examination.

Rollin[31] asks why, by 1930, the Darwin-Romanes approach to mind had virtually vanished from mainstream scientific activity, whereas Darwinian biology had flourished. He believes that the denial of instinct, authenticated anecdote, subjectivity and animal consciousness which took place was philosophically flawed and also in some ways dishonourable. No experimental or logical arguments could be found; rather, the promising Darwin-Romanes position had been swept out of fashion by rhetorical, sociological, philosophical and valuational factors, being 'caught in the brushfire of positivism, behaviourism, and empiricism which swept through Western thought, cauterizing it, simplifying it, reducing it, and purging it of metaphysical, valuational, and non-empirical taints', an effect still in evidence over half a century later. There were no Kuhnian crises or fatal flaws. Instead, and in common with other areas of cultural life, it suffered from a somewhat indiscriminate reaction against 'embellishment', which in the case of science and psychology was spearheaded by positivism and behaviourism.[32] In fact, 'instinct' as an unfashionable concept did not disappear: it merely became referred to under different terminology as 'motivation' and 'maturation'.

Midgley[33] believes that the increasing specialization which went with the professionalization of science contributed to a relegation of the Darwinian position.

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[30]Richards, R.J. (1977) op. cit., pp.31-2. McDougall viewed purposive striving as a fundamental category of psychology and believed that the energy for such striving springs from the instincts: these cannot be defined in terms of stimuli and responses but are intimately related to emotions (Dewsbury, 1984, op. cit., p.312).
[31]Rollin, B.E. (1989) op. cit., pp.51 & 53.
[32]Rollin (1989) op. cit., pp.67-8, observes: 'One can indeed find elements of this reductionistic, "no frills" philosophy throughout European culture. By the end of the nineteenth century, art, architecture, design, music, and literature had become extremely extravagant ... Much early twentieth-century culture can be seen as an attempt to eliminate or trim away that excess.'
[33]Langley, G. (ed.) (1989) *Animal experimentation - the consensus changes*. Basingstoke: Macmillan Press, p.7.

Hearnshaw[34] felt it ironic that psychology had modelled itself on the mechanistic science that prevailed until the scientific revolution of the early years of this century, but failed until a few decades ago to respond to the implications of that revolution. As a result, philosophical questions have begun to intrude again, as they had in the early years of scientific psychology:

> Psychologists, particularly the new breed of twentieth-century academic psychologists, were remarkably slow to respond to these challenges. Many of them were more interested in experimentation on rats and other animals, where old-fashioned methodology could be applied, than in considering the difficult problems of human psychology. They ignored, or brushed aside, the criticisms philosophers were making, and indeed had been making since the early days of experimental psychology.

E.S.Russell had recognized the questionable state of the methods of study of animal behaviour in his presidential address to Section D of the British Association in 1934: '... it is time biology shook itself free from the limitations imposed upon it by a blind trust in the classical doctrine of materialism. This doctrine is not in harmony with the modern development of philosophical thought, nor with the modern development of physical science, and it is not well adapted to the study of living things.'[35] He supported the organismal theory, the substitution of the concept of organism (with directiveness of activities) for the concepts of matter and mind.[36] The attraction of behaviourism, and the reason why it led so many academic psychologists away from the promising areas suggested by Darwinian theory, was that it represented a version of envied hard science and at the same time seemed to deal with those philosophical objections to routine psychological methodology which had emphasized that its attempt to study mind were primitive and unreliable (and not its business), as well as unscientific. Behaviourism simply removed mind and philosophers from the picture. But 'behaviourism in its rigorous and original form, which in fact proposed to solve the psychological problem by liquidating its difficult aspects, has itself proved impracticable.'[37]

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[34]Hearnshaw, L.S. (1987) *The shaping of modern psychology*. London: Routledge & Kegan Paul, pp.227-8.
[35]Russell, E.S. (1934a) Presidential address. The study of behaviour. *British Association for the Advancement of Science: Reports*, Section D, pp.83-98.
[36]'From our organismal point of view, the study of behaviour is neither comparative physiology nor comparative psychology; it is the study of the directive activity of the organism as a whole, in so far as that activity has reference to the organism's own perceptual world. It must start with what Lloyd Morgan calls the "plain tale" of behaviour, the full and accurate description of what organisms do, and of what they are capable.'
[37]Humphrey, G. (ed.) (1963) *Psychology through experiment*. London: Methuen, p.12.

Although the potential for development of Darwinian theories for studies in animal behaviour was not actively pursued in Great Britain after Hobhouse, it was not the case that behaviourism took over in their stead. There was, rather, a period of quiet lasting until the Second World War, in which limited work was carried out, some of it showing the influence of the new ideas from across the Atlantic. At the same time, doubts were often expressed publicly about these ideas by scientists interested in the cultural role of experimental psychology and its philosophical and religious implications. J.Arthur Thomson commented:

> The spider has no science of ballistics; it does not individually invent what it does; but an apsychic account appears to us like the play of Hamlet with the part of the Prince of Denmark left out ... All that we are concerned with here is an appreciation of the big fact of mental evolution. As age succeeded age the leading types of animal life along various lines of evolution advanced in bodily differentiation and integration, in mastery of their environment and complexity of interrelations, in freedom and fulness of life. But there was something more; there was a movement towards the emancipation of the Psyche ... Here is a big fact, admitting of religious interpretation, the evolutionary trend towards the increased dominance and freedom of mind.[38]

From the turn of the century it was those naturalists and zoologists increasingly using the term 'ethology' who stepped in to fill the vacuum created by others who became enmeshed in environmental conditioning and learning theories: 'it may be said that the early ethologists shared a distinctive view of animal behaviour and of the way in which it should be studied. This view held that animals possess specific, innate "characters" which can be understood, often by direct analysis with human character, on the basis (analogy ?) of prolonged and sympathetic observation.'[39] The disagreements that later escalated between laboratory-based comparative psychologists and the field-based ethologists, dividing the intellectual resources available to animal behaviour studies, were perceptible from the start. Edmund Selous, a committed Darwinist, was a severe critic of the laboratory methods of the animal psychologists (as well as of the widespread disinterest in behaviour amongst his fellow ornithologists): 'to watch an experiment made by nature is in 9 cases out of 10 much better than to make one oneself.'[40]

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[38]Thomson, J.A. (1925) *Science and religion*. London: Methuen, pp.129 & 132.
[39]Durant, J. (1981) Innate character in animals and man: a perspective on the origins of ethology. In: Webster, C. (ed.) (1981) *Biology, medicine and society 1840 - 1940*. Cambridge: University Press, pp. 157-92.
[40]Selous, E. (1901) *Bird watching*. London: Dent, p.166.

This belief was not then shared by those like Thorndike, who set in motion what was shortly to become an intensive new programme of laboratory studies, at first stimulated by British work but soon to depart along distinctively American lines, being supported and encouraged by the flourishing establishment market for educational research which grew alongside it and which it cultivated and served. The design of Thorndike's best known experiment, that involving cats in puzzle-boxes,[41] was at fault because it did not allow the animals to apply their full problem-solving potential, but his procedure was excellent. The efficiency of the procedure enabled the accurate presentation of exact data concerning stimulus-response curves and the performance of the experimental subjects. The objective testing of animals in this way developed rapidly in the United States of America, and the white rat, first used in behaviour work by Kline and Small at the turn of the century, became the most common laboratory animal.[42] Dewsbury[43] remarks that Thorndike's work in this year had other significance, since he concluded that the principles governing learning were essentially the same for all species, a conclusion which contributed to the decline of a broad-based comparative psychology: it appeared sufficient now to concentrate on studies of the rat, a representative, convenient, cheap and prolific laboratory animal. Thorndike began to encourage the belief that 'an intensive experimental analysis of the effects of reward and punishment in a few species could yield the laws for a general psychology of learning. In this way he contributed to the virtual disappearance for many years of the evolutionary comparative framework.'[44] Furthermore, he suggested a new purpose for experimental psychology: 'There can be no moral warrant for studying man's nature unless the study will enable us to control his acts.'[45] Rollin[46] claims that this moral-valuational pronouncement explains the disappearance of the Darwin-Romanes approach to mind, and the ascendance of radical behaviourism, especially as Watson and Skinner began to articulate the potential in it for control,[47] and with the growing commitment to a unity of science and to reductionistic physicalistic science, behaviourism became ideologically acceptable.[48]

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[41]Thorndike, E.L. (1911) *Animal intelligence (collected papers, 1898-1901).* New York: Macmillan.
[42]Warden, C.J. (1928) op. cit., p.503.
[43]Dewsbury, D.A. (1978) *Comparative animal behaviour.* New York: McGraw-Hill Book Co., p.23.
[44]Jenkins, H.M. (1979) Animal learning and behavior theory. In: HEARST, E. (ed.) (1979) *The first century of experimental psychology.* Hillsdale, New Jersey: Lawrence Erlbaum Associates, p.183.
[45]Thorndike, E.L. (1911) op. cit., p.15.
[46]Rollin, B.E. (1989) op. cit., pp.96-7.
[47]Watson successfully pushed a new philosophy, a new set of values, a new career for psychology, and was selling it, not proving it (B.E.Rollin, 1989, op. cit., pp.97-8), recognizing that control, technology, practicality and progress were respected by scientist and layman and that behaviourism could be proposed as a new force in, for example, education, medicine, law and advertising. Untypically for a scientist, he exploited the popular press, and he showed that his techniques could work, as when he became a successful advertising consultant.
[48]Rollin (1989, op. cit., p.101) comments: 'It is ironic, of course, that while psychology [in the

Evolutionary aspects of animal psychology were therefore increasingly minimized, and did not reappear in strength until the advent of ethological studies of animal behaviour. In this way, having taken the lead in animal psychology from some important sources in Great Britain, American workers then proceeded to construct their own theoretical frameworks and to ignore those influences that had inspired their British counterparts in the first place: the possibilities raised by Darwinian theories remained unrealized on both sides of the Atlantic for some time to come, and comparative psychology became much less comparative.[49]

> The systematic study of animal learning began as part of comparative psychology. Its purpose was to provide evidence for Darwin's thesis that the mental capacities of man, no less than the structure of man, evolved from the lower animals. But as the study of animal learning became increasingly an experimental, laboratory science, it grew away from its comparative, evolutionary beginnings. By the 1940s, in the era of neobehaviorism, many believed that the experimental analysis of animal learning could provide fundamental laws for a general theory of human behavior,[50]

as well as the means to control it. This aspiration had begun with Thorndike, and for the first half of the twentieth century it provided a strong motivating force for American animal psychology that was absent in the UK and which in the USA was condoned by progressive establishment educational interests.

Just as Thorndike's work had been inspired by Lloyd Morgan, so its publication in 1898 encouraged a reciprocal phase of experimental activity in Britain carried out by the last investigator of this early series of influential British comparative psychologists. L.T.Hobhouse believed that the design of Thorndike's experiment did not permit the animals to display their full imitative and problem-solving capacities, or their capacity to learn quickly, since their state of agitation and natural histories had not been taken into account.[51] He found it especially easy to criticize Thorndike's work because the latter's procedure and findings were so well recorded. His experimental design was better than Thorndike's,[52] but his arrangement of methods, procedure, analysis and

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United States] was earnestly attempting to become like physics, the latter was moving away from the positivistic, mechanistic dream towards acausality, possible entities and possible worlds, non-local causation, wave functions and all the other forms of "quantum strangeness" we now take for granted.'

[49]Hilgard (op. cit.) wrote as late as 1960: 'I am inclined to believe that the term "comparative psychology" should be confined to studies carried out in evolutionary spirit, but contemporary practice does not distinguish sharply between those who use animals in one way or the other.'

[50]Jenkins, E.W. (1979) op. cit., p.177.

[51]Hobhouse, L.T. (1901) *Mind in evolution*. London: Macmillan.

[52]Weiskrantz, L. (1985) Categorization, cleverness and consciousness. *Royal Society of London*.

recording failed to match the new rigorous scientific standards of the American,[53] whose work is often considered to mark the beginning of controlled animal experimentation in psychology.[54] Hobhouse's work tackled, with controlled subjectivity, perceptual learning in cats, dogs and monkeys, and he incorporated his findings into an evolutionary theoretical structure that was both parsimonious and comprehensive:[55] his analysis was 'the most comprehensive theoretical exposition of the evolution of learning of its time.'[56] He identified what the later ethologists termed 'releasing stimuli' as the mechanism of instinct. Organisms themselves were not passive or mechanical, but active, assertive, plastic and self-determining, while remaining subject to general requirements of homeostasis. Hobhouse accepted perceptual (rather than merely imitative) learning in animals, which Thorndike's 'law of effect' had rejected; and he also identified the principle of stimulus generalization and learning sets.[57] He presented an extraordinary variety of problems to a wide range of animals, including an otter and an elephant, and influenced both Yerkes[58] and the *Gestalt* psychologist Kohler in the creation of discrimination apparatus and tasks for chimpanzees.[59] Much of the material in *Mind in evolution* (1901) touched on issues that would later be widely considered in the study of animal behaviour, such as the possible purposive nature of animal activity as well as the animal's ability to experience (later *Gestalt*-type) perceptual relationships.[60] Hobhouse proposed that apes and monkeys have a near-human capacity for mastering concrete perceptual relationships, which he called 'practical judgment', and that the capacity for reasoning can be seen even in Thorndike's own data - as in the sudden improvements of the learning curves of individual animals. He himself set tasks of box-stacking and raking-in of food and other objects with sticks and ropes.[61]

Philosophical Transactions. Series B. Biological Sciences, 308: 3-19.

[53]Boakes, R.A. (1984) op. cit., pp.181-2.

[54]Singer, B. (1981) op. cit.

[55]Mackenzie, B.D. (1977) op. cit..

[56]Gottlieb, G. (1979) Comparative psychology and ethology. In: Hearst, E. (ed.) (1979) *The first century of experimental psychology*. Hillsdale, New Jersey: Lawrence Erlbaum Associates, p.162.

[57]Hearnshaw, L.S. (1966) The comparative psychology of mental development. *L.T.Hobhouse Memorial Trust Lecture* no. 36, 5 May 1966, Bedford College, London. London: University of London, Athlone Press.

[58]Yerkes was an American who untypically developed his investigations outside mainstream behaviourism.

[59]Hearnshaw, L.S. (1964) op. cit., p.103.

[60]Boakes, R.A. (1984) op. cit., pp.182-4.

[61]Dewsbury, D.A. (1984) op. cit., p.303. Zusne credits Hobhouse with founding 'the science of phylogenetic psychology,' contending that, in *Mind in Evolution*, he was the first to present a comprehensive treatment of the psychological development of animals by examining the evolution of instinct, habits, and complex processes in a wide range of species. Zusne, L. (1975) *Names in the history of psychology: a biographical sourcebook*. London: Wiley, p.282.

In common with other students of animal behaviour in Great Britain at the turn of the century, Hobhouse supplemented his book writing with articles in the popular press. He contributed a series called 'The Diversions of a Psychologist' to *The Pilot*[62] in which, apart from frequent references to his *Mind in Evolution*, he warns of the unreliability of anecdotal evidence but describes experiments which readers can try for themselves. In these articles Hobhouse analyzes his own work and that of Thorndike, and refers to his studies in learning and imitation carried out at home with his cat and dog, and to his comparison of different species' abilities through work with circus and zoo animals such as elephant, rhesus monkey and chimpanzee, by arrangement with Messrs Jennison, proprietors of the Belle Vue Gardens in Manchester.

Wider contexts and external influences

Status and perceptions of science

The position of science within the British establishment and in society in the several decades leading up to the First World War was not at the time considered to be one of advantage or encouragement. 'Scientist' as a term was of only comparatively recent use,[63] and those who became regarded as scientists, inheriting the role of the natural philosophers, faced the challenge of divesting themselves of the baggage of associations which remained linked to their interests but which were out of place in an era of increasing technological and scientific promise. Scientific activity was associated with the interests of leisured gentlemen and therefore inevitably appropriate only to those who could afford them, such as Darwin himself, Huxley, Galton (Darwin's cousin), Lubbock or Romanes.[64] In the nineteenth century the state only employed zoologists and biologists in museums, although it did help to fund applied laboratory research in the new marine biological stations that began to appear from the 1870s as a result of interests in the economy and resources of fishing grounds.[65]

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62 'A Weekly Review of Politics, Literature, and Learning' (ed. D.C.Lathbury, London): vol.5, January - June 1902.

63 Whewell, W. (1840) *The philosophy of the inductive sciences, founded upon their history*. London: Parker.

64 Cardwell has pointed out that just as Captain James Cook or Nelson would not have been commissioned in the late Victorian Royal Navy, because of their humble working class backgrounds and lack of means, so the cost of education at the turn of the century meant that, for example, science graduates would also come only from that section of society that could afford it. Cardwell, D.S.L. (1972 2nd ed.) *The organization of science in England*. London: Heinemann.

65 Lubbock himself played a leading part in the establishment of the first marine laboratories.

Aspiring career scientists were not admitted to the social or political elite until after the Second World War.[66] By 1916 'Neither the political nor the official mind in this country yet realizes the power which science can give to the modern State; because classical and literary studies still form the chief high road to preferment in Parliament or in public offices.'[67] In 1924, Viscount Knutsford reminded the House of Lords that 'this House contains leaders in almost every branch of life - leaders of religion, of politics, of literature, of business, and of law; indeed, of practically every walk of life - but, unfortunately, we are very poor in this House as regards representatives of science or of medicine'.[68] It had also been noted in *Nature* in 1916 that scientists fared badly in the honours lists. Very different circumstances in the United States were noted by Sir Ernest Rutherford and Commander Cyprian Bridge in their report about their transatlantic visit in the company of the French Scientific Mission between 19 May and 9 July 1917. As a result of this visit, which was made on behalf of the Admiralty's Board of Invention and Research, they became aware of:

> ... the enormous and hitherto unutilized scientific and technical resources which are available in America to an extent at present quite unobtainable in England or France. These resources comprise not only large numbers of highly skilled scientists and assistants with numerous large and well equipped laboratories, but also practically unlimited mechanical assistance for the manufacture of experimental apparatus.[69]

Such comments reflect what has since become identified as a long established declinist view of the state of British science and technology from the late nineteenth century to the present day, but this view has been criticized. Edgerton[70] believes that historians and scientists have exaggerated such a decline, since there has only been a relative decline since 1870, not an absolute one, as inefficient countries have caught up in the intervening period with Great Britain; and that it is important to note population differences when comparisons are made with countries like Germany concerning, for example, the output of science graduates, because Germany's population was 40% greater between 1900 and 1945. Although the USA was investing more that the UK in general research and development at the time of Rutherford's visit, other critical

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[66]Alter, P. (1987) *The reluctant patron. Science and the state in Britain 1850-1920.* Trans. A.Davies. Oxford and Hamburg: Berg, p.215.
[67]'Science in National Affairs,' *Nature* 96, 1915-16, p.195.
[68]In: Dogs Protection Bill. Debate on the Motion for the Second Reading in the House of Lords on Tuesday March 25th, 1924, when the Bill was rejected without a Division. London: HMSO.
[69]'Report by Professor Sir Ernest Rutherford FRS and Commander Cyprian Bridge RN, on Visit to the USA in company with French Scientific Mission, May 19th to July 9th, 1917.' BIR 28208/17. PRO ADM 293/10.
[70]Edgerton, D. (1996) *Science, technology and the British industrial 'decline' 1870-1970.* Cambridge: University Press.

comparisons between Britain and other developed nations have regularly been made by scientists to support their vested interest in better funding, and historians may have accepted their interpretations too uncritically. Furthermore, before, and especially after, the First World War, civil science benefited significantly from the stimulus of research and development for ongoing defence purposes, a fact not always acknowledged by the scientific community or sometimes denied by left-wing scientists such as J.D.Bernal who thought that military spending impoverished civil work. Edgerton believes that the pervasiveness of the techno-declinist position among historians is paradoxically evidence of the high esteem in which scientists and engineers have been held. He also warns that we should not conflate the history of science and technology, especially in relation to economic performance, with the history of research and innovation, which, as they are undertaken, are costs, not benefits, to an economy. Until after the Second World War, when some applied benefits of animal behaviour studies were realized and acted on, such studies fell mainly within the province solely of innovative academic research, and relied on general arguments from part of the scientific community that such work should be supported as pure science for its own sake, offering the prospect of increased knowledge but whose practical applications could not at any given time be accurately predicted.

In spite of the establishment of the importance of science to the state in the First World War, 'science and scientists were not able to overcome their traditionally low status, even by the 1920s and 1930s,'[71] by which time a larger Civil Service was at least beginning to offer (comparatively very poorly paid) career opportunities through its enlarged scientific element. Low public esteem and awareness were inherited problems linked to perceptions of science as an upper class, aristocratic hobby and a 'gentlemen and players' outlook. Amateur status (in its literal sense) was much admired in the nineteenth century, and science was not seen as a profession for the middle classes like medicine, law or the Church. The social and financial unattractiveness of science to those planning a career denied it young recruits who would in addition have had to negotiate an unsympathetic educational system. In giving evidence to the Select Committee on Scientific Instruction in 1868 Huxley stated: 'I think that the spirit of the teaching at our older universities is entirely opposed to the spirit of scientific thought. At present they are hardly to be trusted with scientific education'. In the same period the equally unsatisfactory status of scientific research at Oxford and Cambridge was reflected in the creation of the Association for

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[71] Alter, P. (1987) op. cit., p.221.

the Organization of Academical Study which set out to promote it as a necessary and nationally beneficial function of academic life.[72] Much later a Fellow of the Royal Society wrote in *Nature* in 1915:

> The general public looks upon scientific investigation as a hobby ... [and this attitude was] ... indigenous in the older universities, where there are a large number of college officials intellectually competent to undertake researches, some of whom do and some do not. At Cambridge in my time scientific investigation was the occupation of the leisure of men whose maintenance was provided by the fees and emoluments of teaching. It was as much a hobby as chess or photography. There was no sense of collective responsibility for providing the nation with answers to scientific questions ... The idea of 'making a living' by scientific investigation never reached the surface, though the merit acquired by research might weigh in the appointment to a post for teaching or administration.[73]

'English science was mainly outside the university system and therefore had only an incidental ability to influence academic curricula or policy.'[74] Alter[75] noted that Sir William Crookes P.R.S. attributed the scant regard for science in Britain to the specific mentality of the upper and middle classes, shaped by public schools and Oxbridge: 'The nation's attitude towards science is, I think, largely due to the popular idea that science is a kind of hobby followed by a certain class of people, instead of the materialisation of the desire experienced in various degrees by every thinking person to learn something about innumerable natural phenomena still unsolved.' C.S.Myers as a youth had decided to attempt a scholarship to study natural sciences at Cambridge in 1891, and the precarious circumstances of his preparation reflected the state of science instruction at the time:

> My science master at school knew little biology and less physiology, and in the private tuition which he gave me I used to find him reading my textbook in physiology (Michael Foster's) so as to keep just ahead of me. I left school in 1890 and joined a year's course in elementary biology, chemistry, and physics at St. Bartholomew's Hospital. Thus, hurriedly and poorly equipped, I gained an entrance exhibition, and soon after a foundation scholarship at Caius.[76]

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[72]Roderick, G.W. (1967) *The emergence of a scientific society*. London: Macmillan. New York: St Martin's Press, p.51.
[73]*Nature* 96, 1915-16, p. 453, quoted in Alter, P. (1987) op. cit., p.222.
[74]Littman, R.A. (1979) Social and intellectual origins of experimental psychology. In: Hearst, E. (ed.) (1979) *The first century of experimental psychology*. Hillsdale, New Jersey: Lawrence Erlbaum Associates, p.46.
[75](1987) op. cit., p.223.
[76]Myers, C.S. (1936) Charles Samuel Myers. In: Murchison, C.A. (ed.) (1936) *A history of*

The increase in numbers of specialist scientific societies and associations towards the end of the nineteenth century, the appearance of a system of qualification for grades of membership, and the publication of society journals (such as that of the British Psychological Society from 1904), reflected the wish of the scientific community to differentiate and refine its activities, to strengthen its various identities and to grow and make inroads into academia. But any suggestion that science should become centrally organized and funded or professionalized (on a salaried rather than only on a society membership basis) met with widespread hostility and suspicion in late Victorian Britain, and the only opportunity for those of merit but without means or social standing (such as Spalding) was to seek patronage, especially if their interests lay in new and little known areas. Indeed, some gentlemen scientists resisted professionalization and any prospect of state interference because they feared it would exclude them from their interests[77] or, in the case of public endowment, compromise the dignity of their subject.[78] These conditions for scientific advancement (which were unreliable, because Britain became relatively scientifically backward, as realized at the time of the Boer and First World Wars) were not due to the apathy of scientists themselves, although many, like Spottiswoode, from a position of privilege or for the sake of the independence of science, opposed the principle of greater state involvement. They resulted largely from reactive conditions in the social, political and religious environment. In the second half of the nineteenth century the power and potential of scientific achievement and invention was clear, and as a result it threatened to invest those closest to it with a role in society which might diminish the influence of the upper social classes and of the Church, which was itself sensitive over an identity problem resulting from the debates arising from Darwinian theories. Huxley[79] wrote of his 'untiring opposition to that ecclesiastical spirit, that clericalism, which in England, as everywhere else, and to whatever denomination it may belong, is the deadly enemy of science'. Scientists such as Huxley, Tyndall and Clifford 'in effect appealed to the intellectual equivalent of free trade in ideas with the heady confidence that if scientists could only set their ideals and powers before the public, the requisite

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psychology in autobiography. Vol. III. Worcester, Mass.: Clark University Press and (1961) New York: Russell & Russell, pp.215-6.

[77]Russell, C. (1983) *Science and social change 1700-1900*. London: Macmillan, p.232.

[78]Alexander Strange, Norman Lockyer and Charles Appleton, for example, proponents of endowment, as well as the Devonshire Commission itself, were frequently accused, and also by the limited number of state-employed scientists (aware of their establishment interests), of intrigue, greed, of seeking to subordinate science, or of attempting to divert funds from the government's own scientific departments. In the 1880s the Society for Opposing the Endowment of Research was established, and the term 'researcher' acquired undesirable political connotations in that decade.

[79]Huxley, T.H. (1889) *Autobiography*. In: Engel, L. (1890) *From Handel to Halle: biographical sketches with autobiographies of Professor Huxley and Professor Herkomer*. London: Sonnenschein.

support and recognition would be forthcoming'.[80] But ironically, science found difficulties less with religion and clergy than with a section of society that used religion as a means to delay change: the real state of affairs was that general society had become irreligious in any case: 'Victorian people lost faith in Christianity with a punctiliousness equalled only by those who have found them out'.[81] Furthermore, science achieved this secularization of society through the agency of Victorian Scientific Naturalism,[82] and in late Victorian Britain, according to Turner,[83] a shift in social and intellectual authority from religion to science took place, and 'the primary motivating force behind this shift ... was activity within the scientific community that displayed most of the major features associated with nascent professionalism'.

From around 1875, scientists began to promote their status and that of their activities by moves to professionalization and by countering the effects both of antivivisectionists' success with public opinion and of the inertia of classically educated and often unsympathetic or ignorant politicians: 'Instead of being promoted as an instrument for improving the student morally and bringing greater physical security or personal profit to humankind, science came to be portrayed as a means to create and educate better citizens for state service and stable politics, and to ensure the military security and economic efficiency of the nation.'[84] According to Russell,[85] Darwinism itself was not sufficient to explain the growth of scientific naturalism and therefore secularization: the public was becoming aware of the value of science in terms of public health, manufacture, engineering wonders etc. An increasingly articulate and professionalized scientific community presented science as all-triumphant, and therefore by inference a kind of public substitute for the old religion (from which, perhaps calculatingly, it adapted terminology to emphasize its dominance: 'church scientific', 'nature's cathedral', etc.). At the same time, of course, political interests were also ready to put science to work to support an appropriate political outlook, as when the theory of 'survival of the fittest' was carefully transported into the competitive life of Victorian capitalist society to take shape as 'social Darwinism'.[86]

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[80]Turner, F.M. (1980) Public science in Britain, 1880-1919. *ISIS*, 71, no.259, p.590.
[81]Moore, J.R. (ed.) (1989) *History, humanity and evolution. Essays for John C. Greene.* Cambridge: University Press, p.195.
[82]Russell, C. (1983) op. cit., p.256.
[83]Turner, F.M. (1978) The Victorian conflict between science and religion: a professional dimension. *ISIS*, 69, no.248, p.364.
[84]Turner, F.M. (1980) op. cit., p.592.
[85](1983) op. cit., p.256ff.
[86]Sparks indicates that psychological theory and research interests were linked to the current nature of society. 'When the world was considered to be the manifestation of a Divine Plan, it was natural for people to see animals and their habits as part of that scheme. The advent of evolutionary theory

John Lubbock, although a member of the independent, self-sufficient scientific aristocracy of the late nineteenth century and therefore not typical of or sympathetic with the new utilitarian, professionalizing outlook of part of the contemporary scientific community, contributed through his experimental work to the support of the social ideals and cultural acceptance of scientific naturalism as a necessary part of the moral regeneration of mankind. His analysis and explanation of insect societies, as in *Ants, Bees, and Wasps* was carefully set before as wide a public as possible so that lessons might be learned from insects about social organization and so that the achievement of science in gleaning this information could be properly acknowledged.[87] However, in popularizing his work, he soon shared the common penalty of having it downgraded by some other scientists as unoriginal and lightweight (but not by his fellow comparative psychologists Romanes and Lloyd Morgan).

Hitherto in the nineteenth century, regular state links with officially funded science had been largely restricted to naval and military matters (but Hall[88] accuses Turner of neglecting state use of the Royal Society as a source of regular, if unadvertised and *ad hoc*, general scientific advice). To confuse the situation further, there were protective prejudices against academic traditions not based on classical studies, and schools and universities were blamed for retaining 'medieval' teaching preoccupations. The evidence of C.P.Snow's 'two cultures' model was there: artists, writers and scholars on the one hand, and scientists and engineers on the other. British scientists envied the position of their counterparts on the continent (especially in Germany, where in 1904 the universities received on average 70% of their income from the state) and in the United States, where there was public esteem for science. The establishment of the Imperial College of Science and Technology in the 1900s was a university-based response, but in Britain there was still by then no state science policy or cult of research, and instead only a crude system of payment by results. Witnesses to the

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tended to shift the emphasis away from religious explanations. But some scholars have suggested that the theory of natural selection may have been affected by the climate of laissez-faire capitalism current in the Europe of Darwin's day. For decades after *On the Origin of Species* was published, nature was observed as "red in tooth and claw". But, by the middle of the present century, nature was being viewed more benignly. When searching for possible reasons, it is tempting to suggest that the rise of Behaviorism and the fascination zoologists came to feel for communities and the apparent altruism animals displayed was influenced by the success of Socialism as a political force.' Sparks, J. (1982) *The discovery of animal behaviour*. London: Collins, p.275.

[87] Being nevertheless 'aware of the collectivist ideological uses of social insects, he employed "disinterested" experimentation to cast doubts upon the utopian depictions of co-operative, altruistic communities of ants and bees'. Clark, J.F.M. (1997) 'The ants were duly visited': making sense of John Lubbock, scientific naturalism and the senses of social insects. *British Journal of the History of Science*, 30: 151-76.

[88] Hall, M.B. (1981) Public science in Britain: the role of thr Royal Society. *ISIS*, 72, no.264, pp.627-9.

Devonshire Commission complained at the lack of research activity in Oxford and Cambridge, and drew attention to the teaching distractions which added to the difficulties of staff who might undertake it; and teaching loads were high because there were so few appointments in science, so research was neglected.[89] Frequent, similar complaints were made around the turn of the century about the continuing problems preventing the urgent development of a suitable research environment in the university system. For example, Gore[90] explained: 'For each single man who can discover, there exist many who can teach. But with teaching in addition to research, and all the usual educational machinery - lectures, apparatus, pupils, registration of students, receipt of fees, examinations and marking of papers - it is the testimony of nearly every teacher in science, that he "has no time for research"'. Gore also criticized the anomaly in society in which the Royal Institution spent only about £250 a year on scientific research while the annual expenditure of the British and Foreign Bible Society was over £200,000.[91]

William Johnston's endowment of a chair in biochemistry at the University of Liverpool in the 1900s was remarkable at the time because it was a research chair.[92] The usual position was that minimal staff were drawn away from research opportunities by the burdensome demands of teaching; and if they were able to carry out research work, they had to do so voluntarily and meet related overheads themselves. In 1911, Professor Moore, the first holder of the research chair, criticized university funding and its effects:

> It is much to be regretted that in the financial system of our universities no separate provision is made for the endowment of research apart from ordinary undergraduate teaching. Even where the Charter of the University insists that it shall advance arts, science, learning and education, no provision is made for any separate endowment of research...The result is a perpetual struggle between teaching and research for the partition of a sum of money inadequate to supply completely the needs of both, and in such a struggle research, though equally or even more important, comes off worst because it is usually regarded by administrators as a luxury, whereas teaching is deemed an essential function in the work of a university.[93]

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[89]Roderick, G.W. and Stephens, M.D. (1976) Scientific studies at Oxford and Cambridge, 1850-1914. *British Journal of Educational Studies*, XXIV, 1, p.55.
[90]Gore, G. (1882) *The scientific basis of national progress: including that of morality*. London: Williams & Norgate, p.203.
[91]Roderick, G.W. (1967) op. cit., p.57.
[92]Morton, R.A. (1972) Biochemistry at Liverpool 1902-1971. *Medical History*, XVI, 321-53.
[93]*Researches in Biochemistry*, 1908-11, 1, Harold Cohen Library, quoted in Roderick, G.W. and Stephens, M.D. (1974) Scientific studies and scientific manpower in the English civic universities

British universities received hardly any state support until the establishment of the University Grants Committee in 1919, and prior to the establishment of the Ph.D. degree in the same year there was little training in research.[94] Germany had by the First World War attracted many foreign students, especially from the United States, to undertake research degrees. Great Britain was able to invade this market after and because of the war.[95] But by then British psychology did not meet American research interests, and there was no adequate laboratory facility for it.

The Royal Society moved slowly to accommodate the full aspirations of science, and in the nineteenth century the British Association for the Advancement of Science, founded in 1831, failed ultimately to promote its interests and needs adequately in the public arena.[96] The Association's constitution had required it to encourage systematic scientific enquiry, to develop communications between scientists and to improve its public relations. To begin with, it succeeded in winning recognition of the value of independent but adequately supported pure science to the nation, and it remained ostensibly politically neutral, although through the X-club it managed some effective political manipulation to further its interests. But its performance in public relations faltered in the closing decades of the nineteenth century as it faced criticism over vivisection and the calls for endowment. As new specialist societies and new universities encroached on its other roles, it then began to concentrate on promoting science in education and to attempt to retrieve its effectiveness in public relations as popularizer and apologist in the twentieth century.[97] The establishment of the Educational and Psychological Sections of the Association helped in this respect and also encouraged communications and collaboration between researchers, practitioners and cultivators in those subject areas, which benefited like others from the publication of ongoing work in the *Annual Reports*, and to a lesser extent later in the *Advancement of Science*.[98]

1870-1914. *Science Studies*, 4: 41-63.

[94]Hearnshaw, L.S. (1987) op. cit., p.125.

[95]Farr, R. (1985) *An Inaugural Lecture. Some reflections on the historical development of psychology as an experimental and social science*. London: The London School of Economics and Political Science.

[96]This shortcoming persisted for a long time. In a message from the president, G.P.Thomson, accompanying the first issue in new format of *Advancement of Science* in May 1960, he observed that the proportion of educated people with a reasonable appreciation of contemporary science had hardly risen in the last century and may even have fallen.

[97]MacLeod, R. M. (1981) Introduction. On the advancement of science. In: MacLeod, R.M. and Collins, P. (eds) (1981) *The Parliament of Science. The British Association for the Advancement of Science 1831-1981*. Northwood, Middlesex: Science Reviews Ltd.

[98]Brock, W.H. (1981) Advancing science: the British Association and the professional practice of science. In: MacLeod, R. and Collins, P. (eds) (1981) ibid.

Because of the Royal Society's perceived historic commitment to the application of science for the benefit of mankind and its attempts to agitate for the better recognition and use of science, it had earned the privilege of being responsible for the distribution from 1849 of modest government grants awarded not only on the basis of subject and individual competence but on the basis also of the feasibility of the project and the likelihood that it would produce results.[99] However, its alliance with the establishment, based on an explicit faith in its integrity, and the fear of being identified as politically partisan, prevented the Royal Society from more energetically supporting the science community's demands for better funding for pure as opposed to utilitarian research. Although in 1899, with the creation of the National Physical Laboratory, the state came into a new relationship with science,[100] the government funds administered through the agency of the Royal Society had nevertheless resulted during the previous three decades in a significant increase in the publication within scientific periodicals of the fruits of original research.

A sign of the neglect of science and of those able and willing to develop it came in the form of the X-club, an exclusive, anti-religious and unofficial group of prominent scientists centred on Thomas Huxley which attempted to influence establishment opinion and policies, and both to minimize Government control and to maximize its support.[101] After 1900, the rise of specialization and the development of science at the universities signalled the end of the subtle monopoly of power held by the London scientific societies and the 'Young Guard' of the X-club: influential scientific networks began to revolve more around university departments.[102] A similar role was intended later for the Tots and Quots, first convened by S.Zuckerman in 1931 to promote a social conscience among British scientists and to discuss urgent issues of the inter-war years in relation to scientific response and solutions for social development. One member was Desmond Bernal whose *Social Function of Science* (1939) considered the place of science in society, and the need for public accountability and funding of it: such socialist scientists 'ran headlong into the opposition of the scientific establishment, whose ideology derived from the turn-of-the-century drive to secure for science a place of honour among professional middle class groups.'[103] Other, less

[99]Hall, M.B. (1984) *All scientists now. The Royal Society in the nineteenth century.* Cambridge: University Press, p.160.
[100]Poole, J.B. and Andrews, K. (eds) (1972) *The government of science in Britain.* London: Weidenfeld and Nicholson, p.9.
[101]Russell, C. (1983) op. cit., p.244.
[102]MacLeod, R. M. (1970) The X-Club. A social network of science in late-Victorian England. *Notes and Records of the Royal Society of London*, 24, p.318.
[103]Turner, F.M. (1980) op. cit., p.608. Solly Zuckerman claimed that, although a 'Society for Freedom in Science' was set up to oppose Bernal's views, his book had little effect because few,

exclusive organizations with a political and lobbying role had earlier come into being, such as the British Science Guild of 1904, 'a conservative, social imperialist pressure group seeking to combine the intellectual prestige of science with the political attraction of efficiency and empire';[104] and trade unions including the National Union of Scientific Workers also appeared in the early years of this century, reflecting a new professional self awareness on behalf of science and scientists.

Towards the turn of the century, and after the Devonshire Commission (the Royal Commission on Scientific Instruction and the Advancement of Science) had established (initially with little effect) the inadequate state recognition and funding of science in its economic and educational context in Britain, conditions were set for the gradual rise of technical, vocational and applied science in civic universities, which were to be strongly influenced by the German ideal of *Wissenschaft* as well as by the English ideal of liberal education,[105] and to some extent in Cambridge University: the British university system had so far been based on classical studies, academic conservatism and the neglect of research for the sake of teaching. By 1870 'Germany had about 2000 students reading science and technology, out of a total of around 18,000. Comparable figures to these were not obtained in Britain until thirty years later. Thus it was that Matthew Arnold was able to complain that French universties had no liberty; English universities had no science; but German universities had both.'[106] The curriculum of secondary education was inadequate for science, and, unlike the position in primary teaching, the would-be secondary science teacher had to pay his own training fees. In 1900, the number of day-student science undergraduates per ten thousand of population was 5 (UK), 12.8 (USA) and 7.9 (Germany), and by the time of the First World War there were only about 300 postgraduates in scientific research in England and Wales.[107] At the turn of the century most science graduates opted for teaching, and because more science teaching posts had been made available by 1914 the number of science graduates had begun to increase. This period also saw a revolution in higher education and an increase in the number of academic scientists,

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scientists or laymen, bothered to read it: a passive attitude characterized the vast majority of the scientific world. Zuckerman, S. (1978) *From apes to warlords: an autobiography 1904-46*. London: Hamish Hamilton, p.396.

[104]Turner, F.M. (1980) op. cit., p.602. It was formed by Norman Lockyer as a pressure group for science and scientific method in the public arena, once it had become clear that the British Association was reluctant to sponsor such a focussed campaign. By 1936, when it was absorbed by the British Association, it had managed to improve public awareness of scientific issues in research, teaching and industry. Poole, J.B. and Andrews, K. (eds) (1972) op. cit., p.10.

[105]Roderick, G.W. (1967) op. cit., p.37.

[106]Russell, C. (1983) op. cit., p.238; Arnold, M. (1868) *Schools and universities on the Continent*. London: Macmillan, p.232.

[107]Cardwell, D.S.L. (1972) op. cit., p.215.

but after the war and until the 1950s applied science eclipsed pure, as shown by the occupations of Fellows of the Royal Society before and after the First World War. In the 1910s industrial and commercial need and support had soon led to the better encouragement of applied science for economic, and, shortly after, for military and wartime purposes. But in the absence of a clear, indigenous science policy the progress of organized science was severely interrupted by the outbreak of hostilities: 'The pursuit of science and the training of scientists came to an abrupt halt in 1914 [when it also became unacceptable to admire German universities or anything German]; in this respect 1939-45 was completely different'.[108] But by the end of the First World War circumstances also made it clear that it would no longer be possible to rely on patronage and private means to sustain British scientific activity.

Controversies and uncertainties existed between the late nineteenth century and the beginning of the First World War concerning the relationship between the government and the Royal Society and over the the desirability of endowments and grants.[109] It was precisely at this time that experimental psychology was in its most sensitive and promising phase. Great Britain proved unable in the end to sustain it at a level comparable with the energetic support that formed in the USA. This early, first and formative phase of British experimental psychology was therefore heavily conditioned by restrictive external factors, and animal psychology as a sub-specialization did not fare well. Some members of the Royal Society felt it wrong to encourage and sustain impecunious young men in uncertain forays into scientific research: perhaps modest support would be better invested in independent people of proven capability who would thereby ensure the Royal Society's own independence, autonomy and standing. The Treasury was equally cautious, as shown by its reluctance, until the empowerment of the Department of Scientific and Industrial Research in 1916, to approve state fellowships, and by its reliance instead on the agency of the Royal Society in distributing the government grant as its intermediary. A system of reward rather than stimulus therefore affected research programmes, until the influence of the universities began to increase as they took on greater financial power and accountability in the direction of research and in the support of that specialization and professionalization which had remained unattractive to the Royal Society; and in response to recommendations of the Devonshire Commission in the 1870s, Oxford and Cambridge

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[108]Cardwell, D.S.L. (1972) op. cit., p.221.

[109]MacLeod, R.M. (1971) The Royal Society and the Government grant: notes on the administration of scientific research, 1849-1914. *Historical Journal* 14: 323-58; The support of Victorian science: the endowment of research movement in Great Britain, 1868-1900. *Minerva* 4: 197-230. In: MacLeod, R.M. (1996) *Public science and public policy in Victorian England* Collected Studies Series. Aldershot: Variorum, Ashgate Publishing Ltd.

had begun over the ensuing decades to strengthen the scientific component in university life by allocating college fellowships for scientific research. In other universities and university colleges there were also by 1914 170 privately endowed research fellowships for science. At the conclusion of the war, attention would then turn within the universities to the necessary improvement of the relative position of research training (and research within research schools), as compared with that of teaching and education.

After the Boer War economic competition had grown from other developed countries, especially Germany, and there was a strong economic stimulus for state interest in science.[110] In 1913 the Medical Research Committee was set up (later becoming the Medical Research Council in 1920) to co-ordinate medical and biological research, which also became a possible means of saving government money in the light of the introduction of National Insurance in 1911 and the consequent need to encourage the nation's health, especially concerning tuberculosis. Because of the First World War, the Department of Scientific and Industrial Research was established in 1916, along the lines of the Medical Research Committee, much later in 1964 to be replaced by the Science Research Council and Ministry for Technology. The interest of the state in these measures was, however, focussed on the industry-relevant applications of science. The general level of state support for universities and their research programmes reached only comparatively modest levels by the 1930s: in 1934 it represented 32% of university income (to be contrasted with the state contribution of 70% in Germany of the 1900s).[111] Julian Huxley estimated that in the same year the total spent on research represented 2% of the amount spent on drink, 3% of that spent on tobacco and 12% of that spent on gambling; and only 0.1% of the National Income, compared with 0.6% for the U.S.A. and 0.8% for the U.S.S.R.[112] Although by the end of the First World War the value of state-supported scientific research had been demonstrated, the progress of research was adversely affected in the interwar years by the uncertain economic climate, beginning with government retrenchment soon after the war involving severe cuts to the DSIR's funding. As a result of the industrial depression of the 1920s, undergraduate studies and the creation of new chairs in the arts increased, although of the advanced students, most were studying science subjects. By 1939, there were 10,278 students of science and technology at English universities, a very small increase on the figure of 9,852 of 1922.[113]

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[110] Alter, P. (1987) op. cit.
[111] Bernal, J.D. (1942) *The social function of science*. London: Routledge, p.420.
[112] Roderick, G.W. (1967) op. cit., pp.67-8.
[113] Argles, M. (1964) *South Kensington to Robbins: an account of English technical and scientific education since 1851*. London: Longmans, pp.75 & 77.

After the First World War, the status and the acknowledged importance of science, especially in its applied form, encouraged those who wanted specifically to secure the future of high or pure science in the context of strengthened university-based research. For psychology, this tactic succeeded in the USA: psychologists furthered their discipline by responding to the knowledge needs of society as represented by a political establishment that had become interested in controlled social improvement. At the same time, they managed to create new markets for new products.[114] In Great Britain, the High Scientists, proposed those such as Gregory of *Nature*, should be responsible for science policy, under which pure research could be promoted and could offer direction to those who worked in a different category as inventors or government scientists meeting the pressing needs of industry and society. This argument was used for the next 50 years:[115] it was met by the science quangos, and it perhaps reflected a wish to maintain the independence of science as in the previous century, while taking advantage of the growing state support of the present one. The continuing disadvantage for scientists and their representatives has been their routine inability to have direct access to and influence upon the policy-makers, Select Committees and 'Green Papers' notwithstanding.[116] But at the same time the remote and elite position that high science was supposed to maintain was compromised by the popularization of sensational scientific questions to which some of its practitioners (e.g. J.B.S.Haldane and Julian Huxley)[117] drew attention in the 1920s.[118] In these years greater public attention was brought to bear on the interests of psychologists, too, through the efforts of such as C.S.Myers, who had been Secretary of the British Psychological Society between 1906 and 1910 and who became President in 1920.

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[114]Danziger, K. (1987b) Social context and investigative practice in early twentieth-century psychology. In: Ash, M.G. and Woodward, W.R. (eds) (1987) *Psychology in twentieth-century thought and society.* Cambridge: University Press, p29.
[115]Werskey, G. (1978) *The visible college: the collective biography of British scientific socialists of the 1930s.* London: Allen Lane, pp.38-9.
[116]Poole, J.B. and Andrews, K. (eds) (1972) op. cit., p.22.
[117]Huxley remained commited to the popularization of science and human and animal behaviour, and in 1942 he served on Collins's New Naturalist Board which eventually published over 50 volumes on British natural history. (Huxley, J.S., 1970, *Memories*, Vols 1 and 2. London: George Allen and Unwin Ltd., p.264.)
[118]Werskey, G. (1978) op. cit., p.84. Solly Zuckerman (1978, *From apes to warlords: an autobiography 1904-46.* London: Hamish Hamilton, p.394) wrote of the 'Tots and Quots': 'At another dinner which took place not long after [1932], the topic for discussion was the popularisation of science, when a disquiet, which some of us still voice, was expressed about the way scientific knowledge is presented by the popular press to the public'. Difficulties over the relationship among scientists, the popular media and the public have persisted. J.Goodfield (1981, *Reflections on science and the media.* Washington D.C.: American Association for the Advancement of Science, p.34) asks: 'must the injunction, "Tell the public what we do and how we do it, and how they benefit," always carry the hidden message, "but while you are about it, remember that we may not be very charitable toward the particular person whose work you describe"?'

Myers helped to change the Society's constitution in 1919 in order to broaden dramatically the membership base and extend general public interest in the subject.

Status and perceptions of psychology and experimental psychology as science

In times that were difficult even for branches of science that were well recognized and which had links with the interests of the natural philosophers, the prospects for new sciences were bleak. It is hardly surprising that psychology faced a struggle when more obviously economically important and established science was neglected in the nineteenth and early twentieth centuries. The progress of psychology also relied on those who had a liberal political outlook or who were non-conformist in their religion, such as F.C.Bartlett, who noted: 'At the beginning of the century psychology ... was usually regarded as ... either the sport of rather cranky people or as a serious threat to the dignity of man'.[119] The position of psychology was made even more difficult because it had to establish an identity separate from disciplines with which it had become closely associated and whose disciples were sometimes reluctant to afford it independence and respect.[120] This was especially true of philosophy, although the sharing of academic ground with anthropology did a little to help experimental comparative psychology establish itself as an independent area in its fledgling years, by encouraging the carrying out of measured psychophysical tests in the course of foreign expeditions among 'primitive peoples' and 'savages'. But because late Victorian accounts of science were predominantly reductionist and mechanistic, a 'scientific' psychology was regarded by many as as a threat to the traditional bases of morality, especially on such occasions as when Huxley extrapolated from experiments performed on decerebrated frogs to maintain that the conscious experiences of willing and feeling are ultimately only illusions, the 'symbols' or 'collateral products' of the underlying brain processes. In the period leading to 1910 when Myers had been campaigning for the inclusion of psychology as a subject available for the Cambridge

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[119]Bartlett, F.C. (1955) Fifty years of psychology. *Occupational Psychology*, 29, 4: 203-16.
[120]Referring to the British Association for the Advancement of Science, Myers recalled 'the doubts which were expressed, not so much in words, as in general attitude, by the Committee of Recommendations of this Association when in 1920 it was asked to consider the formation of a separate Section of Psychology. Such hesitation was probably based on several grounds, not wholly on any one of them. Psychology, it must have been realised, is not immediately concerned with *material* phenomena; unlike these, its "subject matter," the mind, cannot be weighed or measured; nor can mind be satisfactorily regarded merely as a blind mechanism'. (Myers, C.S., 1931, Presidential address. On the nature of mind. *British Association for the Advancement of Science: Reports*, Section J, p.181-95.)

ordinary B.A. degree, Dr. Mayo protested to the Senate that it should have any concern for it: psychology was expensive and undesirable, and 'an attempt to explain all mental phenomena by merely physical causes. They were really a degrading of the mind to mere materialism'.[121] Some of those who objected or hesitated were psychologists themselves:

> Early twentieth-century British psychology did not falter, as some have suggested, wholly because of 'the obstructiveness of philosophical sceptics' who fought the emergence of an independent, rival discipline. Rather, these 'philosophical' scruples regarding the problems and approaches appropriate to a science of psychology arose from within the discipline itself, prompted by its volition-centred concern with the practical impact of psychology as applied to ethics, education, and penology, not from external critics.[122]

Olive Wheeler, a philosophical associate of Beatrice Edgell at Bedford College for Women, had examined the 'ejective' element in psychological research, by which a psychologist would attempt to understand the behaviour of another organism on the basis of analogy and attribution derived from one's direct personal experience of reactions to the environment .[123] She identified the consequences of 'objective' and 'subjective' research:

> Now, if it be admitted that it is the business of the psychologist to collect data of the external behaviour of organisms and not to interpret them in the light of his own subjective experiences, the science does become objective, but in gaining its objective character it loses all that constitutes its claim to a separate existence as a science of mind. A science of outward behaviour is in no way distinguishable from physiology. The only other alternative is to admit that what the psychologist has to do is to interpret the observed outward behaviour of organisms in the light of his own inner experiences. In this case psychology is a science of mind and is distinct from physiology, but it is essentially ejective in character ... it is probably this fact which accounts for the tardy recognition accorded to psychology by some natural scientists.

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[121] In: Crampton, C. (1978) *The Cambridge School. The life, work and influence of James Ward, W.H.R.Rivers, C.S.Myers and Sir Frederic Bartlett.* Edinburgh University: unpublished Ph.D. thesis, p.156.

[122] Daston, L.J. (1978) British responses to psycho-physiology, 1860-1900. *ISIS*, 69, no.247, pp.192, 200, & 207-8.

[123] Wheeler, O.A. (1916) *Anthropomorphism and science. A study of the development of ejective cognition in the individual and the race.* London: George Allen and Unwin Ltd., pp.232 & 234.

Because, unlike physics and chemistry, the environmental sciences were 'soft', they invited scepticism from scientists in other fields: the role of the environment and the history of organisms were necessary considerations, and explanations would therefore have to depend on inexact and experimentally irreproducible space and time dimensions.[124] Later, the change from evolutionary studies to those on learning in the laboratory reflected acknowledgement of this problem. But it was ironic that at the end of the nineteenth century the government was prepared to lend some of its scarce support to applied scientific activity of a 'soft' kind: while the new generation of Huxley's 'modern' biologists was stressing the importance of pure laboratory based morphology, governments were becoming interested in scientifically unfashionable field studies because these offered the only way of monitoring the increasingly obvious changes in natural populations such as fish stocks.[125]

For the most part of the nineteenth century energies that were generally directed to the study of the behaviour of animals were taken up by those whose interests were restricted to recording and collecting; activities which were followed at first mainly by a privileged few as a later equivalent to the Grand Tour, when interests in nature began to match well-established ones in antiquities, and then by a mass of ordinary people reacting to possibilities presented by better education, improved leisure time, affordable amateur photography and greater access to the countryside occasioned by mechanized transport, better roads and the increasing use of bicycles. The growing general interest in nature was exemplified by the new pastime, firmly established in the 1900s, of putting out food for birds, a popular national activity which has persisted. Each category of enthusiast consisted mainly of amateurs and reinforced associations with amateurism, an honourable status but not one useful at that time for the development of studies in the same areas of interest that required the strength of vocational science based on specialized education and research. These amateurs were invariably proud of their status and protective of it. In retrospect, they managed to avoid the 'creeping professionalization' that occurred in French science in the second half of the nineteenth century, where the intention was 'to raise the academic status of the life sciences by deliberately degrading fieldwork and arguing for laboratory-based research.'[126] Furthermore, the natural history movement in Britain of the nineteenth century strongly reflected the taxonomic approach to animal and plant life which was

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[124] Bowler, P.J. (1992) *The Fontana history of the environmental sciences*. London: Fontana Press, pp.5-7.

[125] Bowler, P.J. (1992) ibid. pp.316-7.

[126] Fox, R. (1980) The *Savant* confronts his peers: Scientific Societies in France, 1815-1914. In: Fox, R. and Weisz, G. (eds) (1980) *The organisation of science and technology in France 1808-1914*. Cambridge: University Press, p.265; Russell, C. (1983) op. cit., p.234.

shared by those who often failed to accept the full implications and potential of Darwinian theory, whether in terms of physiological or mental evolution and continuity.

Lloyd Morgan[127] said that in the 1860s he 'was a bit of a boy-naturalist, collecting most things, but with an itch to get at the "go" of them outside the cabinet shelf ... I was an observer of birds and learned something of their song-notes, plumage, and manner of life'. His interests were therefore unusually sophisticated, and reactions to the general state of affairs were considerably delayed. For example, it was not until 1932 that the Society for Experimental Biology was established by Haldane, Hogben, Huxley and Crew 'to make their discipline a more exacting, hard-edged and experimental one; compared to the more descriptive, taxonomic and historical approaches of the pre-war era.'[128] Another investigator in advance of his time had been Lubbock, who as a zoologist had written 'as one of the first to realize that it is what animals do that makes them interesting, and that the whole of classical taxonomy and anatomy and physiology is not an end in itself but an instrument for the understanding of their behaviour. He was also the first to appreciate that behaviour is only explicable in terms of the information animals receive from their environment.'[129] This outlook of Lubbock did percolate into the wider world. The Education Act of 1870 and Huxley's recommendations on the teaching of natural history also helped to promote 'nature study' as a foundation for formal science in schools. Teachers took account of Lubbock's approach to the subject by examining the behaviour of animals and plants, and so nature study became the grandchild of Darwin because Lubbock had been influenced by Darwin personally and because of his interest in the environmental influences on behaviour.[130] But at the same time, publishers began to exploit the growing interest in natural history in ways that were not particularly helpful for science: the popular and commercially efficient attractions of light-weight sentimentalism and anthropomorphism actually produced reactions against objective scientific approaches in biological studies. Julian Huxley later helped to redress the balance by promoting mass interest in real science with *The Science of Life* (1930), which contained a long chapter on animal and human behaviour, including normal and abnormal psychology, and brought 'the facts and implications of biology, including human biology and psychology, before a public already bewitched by physico-chemical

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[127]Lloyd Morgan, C. (1930) *The animal mind*. London: Arnold, p.239.
[128]Werskey, G. (1978) op. cit., p.103.
[129]Pumphrey, R.J. (1958) The forgotten man - Sir John Lubbock, F.R.S. *Notes and Records of the Royal Society of London*, 13: 49-58.
[130]Allen, D.E. (1994) *The naturalist in Britain: a social history*. 2nd ed. Princeton, New Jersey: Princeton University Press, p.180ff.

science and its technical results ... its effects are still manifest in the increased space alloted to biology in the educational curriculum, and the greater interest of the general public in biological facts and their consequences.'[131]

Prospects for experimental psychology as an applied, 'useful' science were not recognized in the late nineteenth century, partly because the status of applied sciences had not become established and made respectable as a result of necessity, and partly because under the conditions of the time psychology was the 'wrong' kind of science. Even the better established pure sciences had fared badly in the economic and social climate of the nineteenth century. Comparisons now might also be drawn with other sciences that won recognition and support only with difficulty, yet which were then in stronger positions than psychology, such as physiology or biochemistry; and because it was not allied, either, to traditional areas of study at Oxford and Cambridge, it fell between two stools before the First World War, after which psychology as an applied science became better recognized and established, owing to its contribution to such problems as shell shock and personnel selection.[132] By then, the distinctive offerings of psychology had become more generally apparent, and it was beginning to fulfil the criteria that Danziger[133] has identified for recognition in the public arena, namely that:

> ... its products must have become clearly distinguished from the everyday or common knowledge and belief of the lay public and achieved the status of expert knowledge ... The very artificiality of laboratory situations became a plus in establishing the credentials of knowledge claims emanating from this source, and the imposition of a numerical form on otherwise trivial knowledge gave it an apparent significance with which lay knowledge could not compete. Replacing ordinary language with jargon helped too.

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[131] Huxley, J.S. (1970) op. cit., pp.169-70. He also participated in the production of a number of 'biological films', such as *Animal Legends. The Mind of the Black-headed Gull*, referred to in *British Association for the Advancement of Science: Reports*, 1939, p.48.

[132] For example, during the First World War Charles Spearman was seconded for at least three months to the Admiralty's Board of Invention and Research, which paid *pro rata* his annual professorial salary in University College London of £400, in order to pursue work with the approval of the naval bases HMS Excellent and HMS Vernon on the 'personal factor' including quickness of perception, acuity of vision, localization of sound, nerve reactions etc. (Memorandum of Preliminary Meeting of Sub Committee, Section II, BIR, held on 8 January 1918. PRO ADM 293/11.) On his return to University College, at a meeting in 1919 to consider the needs of his department, he recalled: 'Already at the outbreak of the war, our laboratory was full of as much work as it could hold. And the war appears to have caused a very great development of the practical applications of this science. Previously these had been almost confined to education and medicine. There is now being opened to it a field of surprisingly large dimensions, particularly industrial and sociological'. Univ Lond. UCL MS Lib. UCL Hist: VI A/2.

[133] Danziger, K. (1990) *Constructing the subject. Historical origins of psychological research.* Cambridge: University Press, pp.184 & 185.

C.S.Myers had identified the particular difficulties faced by psychology in working towards this status, occasioned by other scientists:

> ... as each scientist carries his mind about with him, be he mathematician, physicist, zoologist, physiologist, physician or educationalist, he has always himself felt competent to speak from every-day experience on psychological problems without previous systematic training in the subject, sometimes thus advancing, but probably as often retarding, its progress and its reputation, and always suggesting by such intrusion that psychology neither possesses nor needs any special discipline of its own.[134]

Status of comparative and experimental animal psychology in societal, scientific and psychological contexts

The potential of the German university system in which research was encouraged and based around professors whose lives were not dominated solely by teaching commitments began to be acknowledged at the end of the nineteenth century, especially as the scientific and technological advancement that resulted posed an economic and military threat, but for British comparative psychology,

> ... there was no scientific community in the university - either students or colleagues - who were trained and prepared to exploit ... new ideas and discoveries, whereas in Germany there were ... The English empirical tradition fell on bad times; there was a quixotic surge of popularity of German idealism in England at about the same time it began to falter in Germany. The result was that psychology remained a discipline of verbal analysis in Britain for many years. That kind of analysis is more compatible with naturalistic and mathematical approaches as compared with experimentation.[135]

Among those who studied in Germany were some British students of philosophy and psychology who later brought home and implemented the research ethic as best they could. On a limited basis, therefore, British strengths in theoretical development began to be matched to a very modest extent in the new century by some pure research, and better use of the laboratory for teaching, by those who started or argued for research-based work in experimental animal psychology. But the advantages of the German system were also recognized by those of other nations who not only supplied

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[134] Myers, C.S. (1931) op. cit.
[135] Littman, R.A. (1979) op. cit., pp.68-9.

students but who were also ready to support these students in their research aspirations on their return. In the USA an interest in experimental animal psychology and the refinement of laboratory technique was matched by that country's adoption of the German research ethic and the drawing on British theoretical contributions of the late nineteenth century, theories developed by keen minds operating in unhelpful academic contexts. Soon after the turn of the century, the German form of qualitative research in humans, based on individuals, led, with the aid of British methods such as Galton's anthropometry and Pearson's biometrics, to a quantitative research approach in the USA, when groups and statistics were considered in the examination of, for example, learning theory, and when variables could be experimentally introduced to give comparative data suggesting the explanation of practical problems. This development in the USA was much driven by the wish to apply psychology to social needs, and especially in the area of learning theory an important and lasting opportunity for secure advancement was given to animal studies that began often to take the form of technological research concerned with basic processes; and whereas in Great Britain philosophical attitudes hampered the progress of the subject, they condoned it in the USA. Its vast education industry has been described as the powerhouse of the rapid growth of applied psychology in America.[136] But the result for Britain was that in the face of inadequate funding and support for new university departments, laboratories and facilities a 'brain-drain' occurred and would-be research academics such as McDougall and Titchener, if they had not already given up their interests at home, left to more supportive and challenging academic environments abroad. Having studied physiology under J.S.Burdon-Sanderson at Oxford and investigated the colouration of birds' eggs and the feeding behaviour of birds, Titchener had proceeded to Leipzig in 1890 to study for his Ph.D. under Wundt. He returned to Oxford briefly but failed to persuade the university to offer him an appointment so that he could introduce the 'new psychology' into the curriculum, and left to take up a psychological appointment at Cornell, where, in the manner of Sir Frederic Bartlett later at Cambridge, he became the inspiration for students who would later set up laboratories of their own, meanwhile producing a prolific quantity of theoretical and research papers.[137] He stated that for him 'the laboratory is all-important, the vital centre of the whole department, the source of inspiration, instruction, training and scientific advance for undergraduates, graduates and instructing staff. I gave up Oxford for Cornell solely because Cornell offered me a

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[136]Danziger, K. (1987b) op. cit., p.26.
[137]Tweney, R.D. (1987) Programmatic research in experimental psychology: E.B.Titchener's laboratory investigations, 1891-1927. In: Ash, M.G. and Woodward, W.R. (eds) (1987) *Psychology in twentieth-century thought and society.* Cambridge: University Press.

laboratory.'[138] He had earlier remarked: 'I was impelled toward experimental psychology by dissatisfaction with the logical constructions of the English school.'[139]

The few years flanking the turn of the century therefore witnessed a curious irony in the development of experimental techniques in animal psychology. Although the work of British scientists had reached a point when the refinement of their thought and methods could have provided the basis for a new, systematic programme of experimental comparative psychology in Britain in the new century, the fruits of this work served only to assist the establishment of such a programme (but one with a much modified emphasis) in the United States of America, while the opportunities at home were largely ignored. Later it was recognized that an autonomous scientific tradition of comparative psychology had never developed in Britain.[140] Tinbergen saw complex reasons for this failure:

> The existing branches of biology, to which genetics had in the meantime been added, attracted the available talent; there were relatively few biologists, and their science did not have much of a status even in scientific circles; behavioural phenomena were too complex to yield easily to exact description, let alone to experimental analysis; above all, perhaps, religious attitudes hampered scientific analysis of animal behaviour, so uncomfortably reminiscent of our own.[141]

Although Hobhouse's short-lived experimental work, much of it carried out at Manchester's Belle Vue Zoological Gardens, represented the most highly developed phase of British comparative psychology and inspired several later, foreign workers, his influence in Britain had no material effect, and he was not remembered for his animal work once the First World War had got under way and he had turned to sociology at the London School of Economics. After Hobhouse 'no-one took up the work so brilliantly commenced. The virtual cessation of this promising line of development is perhaps one of the most lamentable occurences in the history of British psychology.'[142] In 1908, only sixteen copies of Lloyd Morgan's *Habit and instinct* (1896) were sold in the United Kingdom.[143] But in the United States of America,

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138 Titchener to Harvard's President Lowell, 13 June 1917. Department of Manuscripts and University Archives, John M.Olin Library, Cornell University.

139 Titchener, E.B. (1901-1905) *Experimental psychology, a manual of laboratory practice*. New York: Macmillan, Vol. 1, vii-viii.

140 Flugel, J.C. and West, D.J. (1964) *A hundred years of psychology 1833-1933 and part 5 1933-1963*. 3rd ed. London: Duckworth.

141 Tinbergen, N. (1973) *The animal in its world. Explorations of an ethologist 1932-1972. Vol.2. Laboratory experiments and general papers*. London: George Allen and Unwin, p.131.

142 Hearnshaw, L.S. (1964) op. cit., p.104; (1969) op. cit., p.7.

143 Boakes, R.A. (1984) op. cit., p.51.

where experimental procedure had become properly established on a scientific basis and where, in contrast with the Britain of the end of the previous century, it ranked at least as highly as experimental design and hypothesis, the new period of extensive and exhaustive enquiry in animal psychology had begun.

This new period was significantly characterized also in the USA by a very considerable investment and expansion in education, governed by an ideology of rationalized efficiency to which American experimental psychologists such as Thorndike gave a calculated, strategic allegience. Educational decision-makers and administrators adopted American experimental psychology to guide and validate education policy, and this new 'market' provided it with a secure, professionalized future, further strengthened by military requirements for applied research in the First World War.[144] An important facet of American educational research was the study of animals to develop theories concerning basic learning processes. Such studies became part of institutionalized American science and veered away from and left behind the antecedent groundwork that had been developed in Great Britain, where the domestic administrative climate for such secondary developments did not exist.

It has been suggested that one reason for the failure of British comparative psychology, in contrast, to become organized and institutionalized was the conservatism and antipathy of the university establishment.[145] This attitude continued into the 20th century, and was altered to a limited extent only after the practical worth of other forms of psychology had been shown when applied to casualties of the First World War, or when at the same time psychological techniques were applied to training in matters such as flying or submarine detection.[146] Nevertheless, as early as 1881, the year before his death, Darwin himself had published the results of forty years of intermittent experimental research and observation of what promised to be the agriculturally and horticulturally beneficial behaviour of earthworms, work which could with justification have been regarded as a sound basis from which to profit from applied animal psychology, if such a concept had been recognized and isolated at the time. Earthworms were then considered a pest deserving of extermination, but

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[144] Danziger, K. (1987b) op. cit.
[145] Hearnshaw, L.S. (1964) op. cit., p.208.
[146] C.S.Myers was appointed Consultant Psychologist to the British Armies in France in 1916, and frequently appeared as an expert witness in court-martial cases concerning a soldier's degree of responsibilty for desertion or for other serious infractions of discipline. In the last year of the war he devised tests and supervised their application for the selection of men suited to hydrophone work for submarine detection. (Myers, C.S., 1936, Charles Samuel Myers. In: Murchison, C.A., ed., 1936, *A history of psychology in autobiography*. Vol. III. Worcester, Mass.: Clark University Press and, 1961, New York: Russell and Russell.)

Darwin's examination of their potential for intelligence represented a research activity with promise for the practical application of new knowledge.[147] Much later, Katz[148] refers to an article in the *Observer* of 30 June, 1935 describing attempts to train sea-lions (with their sensibility to underwater vibrations) to discover enemy submarines in the First World War: 'At great expense the animals were trained first at public swimming baths and later at Lake Bala in Wales, before going on active service in the Channel. The animals' normal subjectivity was, however, negatived by their temperament, the majority deserting in favour of chasing herrings rather than detecting the inedible U-boat'. Seagulls were also trained less successfully for the same purpose, by encouraging them to detect a submarine by releasing food from a dummy periscope. Although the involvement of the scientist and psychologist in the First World War was significant, and generally seen to be so, and the use and organization of science would thenceforward be taken more seriously, the Services were often less than co-operative and regarded such involvement as intrusive.[149]

But in accordance with British tradition, support for science in the form of staff, laboratories and equipment remained largely inadequate, and as far as psychology was concerned, compared very unfavourably with other western countries.[150] In 1914 there were small psychological laboratories only at Cambridge, London, Manchester, Edinburgh and Glasgow. Research and experiment in comparative psychology did not cease after Hobhouse, but the form it took changed, and as facilities slowly grew for practical work it became clear that Britain no longer had many ideas in this area to export, and was prone rather to foreign influence. In the USA, on the other hand, such foreign influences could be claimed to be the country's own, since its cosmopolitan society produced scientific benefits resulting from the variety of new immigrant cultural, scientific and educational influences absent from Britain, where similar advantages were realized only later in different circumstances with the arrival of refugees escaping Nazi Germany.[151]

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[147] Darwin, C. (1881) *Formation of Vegetable Mould Through the Action of Worms*. London: Murray; Romanes, G.J. (1881) Mr Darwin on the work of worms. *Nature*, vol.24, 13 October; Edwards, C.A. (1981) Charles Darwin and earthworms. *Nature*, vol.293, 8 October.
[148] Katz, D. (1953) *Animals and men: studies in comparative psychology*. 2nd ed. London: Longmans, p.47fn.
[149] Poole, J.B. and Andrews, K. (eds) (1972) op. cit., p.12. Sir Solly Zuckerman (*Scientists and War. The Impact of Science on Military and Civil Affairs*. London: Hamish Hamilton, 1966) refers to the uneasy relationship between the scientist and the military man from the Industrial Revolution to the First World War (and in a lesser degree to the present), caused by their different approaches to discipline and order: 'Where it is the habit of the scientist to question, it is that of the soldier to obey'.
[150] Hearnshaw, L.S. (1964) op. cit., p.168; (1969) op. cit.
[151] Two such refugees were Ludwig Koch, who worked with Julian Huxley on animal language in 1938, and David Katz, who had earlier made acquaintance with Manchester University's Department of Psychology as visiting professor before arriving from the University of Rostock in 1936. He

Because of the very limited activity in laboratory-based animal psychology in the early years of this century in Britain, the involvement in it of a high proportion of women is especially noticeable. For example, E.M.Smith (later Lady Bartlett) at Cambridge and Beatrice Edgell and Victoria Hazlitt at Bedford College for Women supervised, carried out or published on experimental work. The reason for the relatively strong presence of women in this rare form of academic activity may have some significance beyond coincidence. The position of women scientists at that time was still insecure, as witnessed by the recent struggle for their recognition in medicine and by the restrictive policies of the Royal Society, shown for example in the case of the physicist Hertha Ayrton, unsuccessfully proposed as a candidate for the Fellowship in 1902, and who marched in the science section of the great suffrage procession of 17 June 1911, which included 800 women graduates wearing academic dress.[152] Norman Lockyer supported Hertha Ayrton's candidacy and in his journal, *Nature*, wrote in favour of the admission of women to the learned societies, but it was generally argued that a university education in science would be useful only to make better wives and mothers, and that the biological sciences were most appropriate because of women's 'capacity for noting details - patience and delicacy.'[153] Women had begun to participate energetically in the natural history field clubs in the mid nineteenth century, and by the century's close unease about this had given way to full acceptance of their amateur involvement.[154] However, academic exertion was claimed to be a source of danger to women's health, and this view, whether contrived or genuinely held, persisted into the present century. One practical result was that 'the exclusion from the learned societies of those few women who went beyond the dilettante pursuit of their interest was in itself a strong disincentive to research, for it was usually only through the various Transactions that findings could be published.'[155]

Huxley's apparent support for female education and access to the professions was contradicted by his opposition to the acceptance of women into the scientific societies, and at least one present-day author, perhaps applying too energetically modern

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thereupon helped to found the Institute for the Study of Animal Behaviour, but soon left for a professorial appointment in Sweden.

[152] Mason, J. (1991) Hertha Ayrton (1854-1923) and the admission of women to the Royal Society of London. *Notes and Records of the Royal Society of London* 45 (2): 201-20.

[153] Macleod, R.M. and Moseley, R. (1978) Breadth, depth and excellence: sources and problems in the history of university science education in England, 1850-1914. *Studies in Science Education*, 5: 85-106.

[154] Allen, D.E. (1994) op. cit., pp.148 & 150-152.

[155] Richards, E. (1989) Huxley and woman's place in science: the 'woman question' and the control of Victorian anthropology. In: Moore, J.R. (ed.) (1989) *History, humanity and evolution. Essays for John C.Greene*. Cambridge: University Press, p.257.

perspectives which were not so fully recognized at the time in question, attacks him for never having used his

> ... unparalleled opportunities, professionally or publicly, to advance the cause of women's higher education, to which he was supposedly so devoted, in any practical way ... He not only used his considerable professional powers to exclude women from organized science, but, in conjunction with the leading Darwinians, he also subtly reinforced late-Victorian assumptions of white male supremacy and contributed to the scientific anti-feminism that characterized evolutionary biology and anthropology in this period. In effect, Huxley excluded women from science in the name of science and redefined that science to ratify their exclusion.[156]

Although the Sex Disqualification (Removal) Act of 1919 opened many professions previously closed to women and ensured that bodies such as the universities or the Royal Society, which were governed by statutes or charter, could no longer use these in support of policies discriminating against women, it was still often implied that women who concentrated their energies on academic attainment for its own sake were unnatural, and that an unsuitable way of life of this type could result in infertility and therefore in an inefficiency of particularly Darwinian significance. 'Almost inevitably, those who emphasized the importance of motherhood in evolution went on to argue that educational arrangements should be geared first to the role of women as mothers.'[157] Furthermore, by the early 1900s, concern for the physical health of the nation had been stimulated by the 'evidence' of national physical deterioration revealed during recruitment for the Boer War; and, together with the pervasive influence of eugenic and social Darwinistic ideas about the need to preserve the quality of the Imperial race, there grew a call for renewed emphasis on the 'traditional' role of women as wives and mothers. The most significant changes in the science curriculum of girls' secondary schools in the later inter-war years were undoubtedly the gradual replacement of botany by biology and the development of courses in general science.[158] Then 'During the 1950s girls came to be regarded as part of a pool of

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[156]Julian Huxley also dealt with the position of women in society by drawing on analogies with bird societies. (Richards, E., 1989, ibid., pp.254 & 279.) This is fully discussed by Bartley, who believed that his views on the mating behaviour of grebes 'were intimately connected to his political and social beliefs for the improvement of humans. It is no coincidence that his public lecture [at the Rice Institute in Texas in 1916] emphasizing equality of the sexes was given in the midst of the active suffragist movement in both the United States and England in the 1910s'. (Bartley, M.M., 1995, Courtship and continued progress: Julian Huxley's studies on bird behaviour. *Journal of the History of Biology* 28: 91-108.)
[157]Dyhouse, C. (1976) Social Darwinistic ideas and the development of women's education in England, 1880-1920. *History of Education*, vol.5, no.1: 41-58.
[158]Jenkins, E.W. (1979) op. cit., p.38.

untapped scientific ability and the differentiation of the science curriculum between the sexes received renewed attention.' However, 'Census data show that, despite the transformations which have taken place in society during the twentieth century, the proportion of women with scientific qualifications in the various age groups altered little between 1925 and 1965, except in the case of medicine, and several studies have highlighted the ambivalence of mid-twentieth century society about the reconciliation of domestic and occupational responsibilities in the education of girls.'[159]

Of Beatrice Edgell (1871-1948) it was said in her obituary: 'Perhaps it would not be unfair to say that she was a Victorian who had managed by intellectual conviction to adjust, at least intellectually, to a very different world from the one to which she herself by upbringing belonged.'[160] In a printed but apparently unpublished article of c.1910-12,[161] she examined the hard-won position of women in the newer English universities and the University of Wales in terms of studying, teaching, legislation and administration. Then she dealt with the problem of over-work and the special threats she believed it posed for women academics and students (echoing the pronouncements of Romanes, referred to below). Solutions might include the provision of more fellowships and studentships to facilitate relief from teaching for the sake of research, and the influence of public opinion through the National Union of Women Workers:

> In any University where the life is open to men and women on equal terms, women are bound to resist any effort to attach to their teaching a scale of payment lower than that in use for men. They must resist this or abjure the very faith which has opened the gates of University life to them - belief in the meaning and value of University training ... The danger of this evil does not lie within the Universities themselves, but in the insidious influence of popular ideas concerning woman's labour.

However, at the time of Beatrice Edgell's retirement it may have been the unattractive salary that caused difficulties in recruiting staff to take on duties in psychology. The Appointments Committee decided to raise the starting salary offered for a readership to a maximum of £600 per annum: this did not compare very favourably with the salary of C.A.Mace whom the Committee had decided to head-hunt - at St. Andrews he earned £550 as a lecturer, and made it clear that he would expect to be paid more than the £600 and then to progress to £700 or £800.[162]

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159 Ibid. p.39.
160 Smith, M. et al., (1949) Obituary notice: Beatrice Edgell, 1871-1948. *British Journal of Psychology*, XXXIX, 3: 121-2.
161 Part of the papers of Henrietta Busk. RHUL Archives, PP1/4.
162 Emergency meeting of the Appointments Committee, 24 February 1933. RHUL Archives, AR 332/6/3.

Perhaps experimental animal psychology was seen as a means to gain a foothold in a new area of science not yet subject to male exclusivity. After graduating in philosophy in the 1890s Beatrice Edgell for one had experienced the German concentration on research and experiment as a student of psychology under Kulpe at Wurzburg between 1899 and 1901, and complemented this with an interest in animal psychology having been inspired by hearing Lloyd Morgan lecture. For her and others with interests that included comparative psychology it may have been that they attempted to adopt, by necessity as well as from choice, a new subject such as this in order to make an impression on the British scientific establishment: at the turn of the century it was still difficult for women to study the classics at universities but scientific subjects were not so firmly established as male preserves.

The participation of women in American psychology from the turn of the century was also relatively high when compared with other areas of science. It has been suggested that the new discipline was prepared to admit them more readily in order to swell its ranks, but half the participants had been faced with the decision to place their career above marriage prospects and others were dissuaded from career aspirations because of expectations of unmarried women regarding traditional duties as carers in the family, for example by looking after the family home on behalf of aged parents. Of those who became professionally involved in psychological work, the tendency was for them to be restricted to the more humble occupations within applied psychology (especially the 'helping' areas unattractive to men) rather than to achieve the more prestigious academic appointments.[163] Social obligations were in evidence in England, too. On her marriage to the Cambridge psychologist, Frederic Bartlett, E.M.Smith, for example, gave up her pioneering studies of laboratory-based animal psychology for the sake of her domestic role. Others, such as Beatrice Edgell and Victoria Hazlitt, pursued their careers as spinsters, and nearly all of their students at Bedford College for Women abandoned psychology on graduating. In the USA in 1906, 22 of 186 psychologists in *American Men of Science* were women,[164] and of these half remained unmarried and usually completed life-long careers as psychologists.[165] As in Great Britain, and untypically of scientific societies, women were accepted into membership of their professional association from the earliest stages, and in both countries their memberships developed into proportions of the whole which were unusually high.

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[163]Furumoto, L. (1987) On the margins: women and the professionalization of psychology in the United States, 1890-1940. In: Ash, M.G. and Woodward, W.R. (eds) (1987) *Psychology in twentieth-century thought and society*. Cambridge: University Press.
[164]Cattell, J.McK. (ed.) (1906) *American men of science: a biographical directory*. New York: Science Press.
[165]Furumoto, L. (1987) op. cit.

Women in the American Psychological Association in 1917 comprised 13% of its membership, a higher percentage than in any other American scientific society. By 1921, the proportion of women psychologists listed in *American Men of Science* was 20.4%, and in 1938, 21.7%; these proportions in scientific areas of activity were surpassed only in nutrition.[166] The proportions of women members of the American Psychological Association were in 1923 18%, in 1928 34% and in 1938 29.6%.[167] Comparable figures for the British Psychological Society show that in 1921 women comprised 31% of the membership (all categories), in 1930 33% and in 1940 37%.

Within a decade or two of the new century the role of women in this and other areas of science became recognized, if not actively encouraged by conditions under which British science was managed. The percentage of women members of the British Psychological Society grew steadily and compared very favourably with those of other professional scientific organizations, Beatrice Edgell becoming President in 1929, and in 1932 President of the Psychology Section of the British Association for the Advancement of Science. For such reasons, and also because he held a leading Darwinist position in Britain in the modern and enlightened study of behaviour, with (somewhat anthropomorphic) reference to animal models, it is highly ironic to note the attitudes of a few years earlier of the comparative psychologist G.J.Romanes[168] to women and the supposed (and commonly assumed) unnatural effect on them of pressures of academic exertion. Within a very short time, after Romanes and other prominent British theorists of the end of the nineteenth century had finished with their own writing and their often imprecise and avowedly subjective research or experiment, these women played a significant part in representing in Britain the modern experimental development of the subject which had been largely lost to the USA. They also helped to maintain in Britain an awareness of American hypotheses and methodology as these were refined, promoted and then sometimes borrowed: the establishment of international links for the subject kept it alive in Britain at its most vulnerable time.

Alongside the sporadic activity of the British comparative psychologists of the earlier part of the twentieth century was that of physiologists, neurologists, zoologists and ethologists in related fields. The mixture of activities, the limited resources and the lack of opportunities for co-operation and co-ordination meant that no enduring

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[166]Rossiter, M.W. (1982) *Women scientists in America: struggles and strategies to 1940.* Baltimore: Johns Hopkins University Press, p.50.
[167]Rossiter, M.W. (1982) ibid., p.278.
[168]Romanes, G.J. (1887) Mental differences between men and women. *Nineteenth Century*, May edition.

schools of thought took shape. Through circumstances rather than intention no demanding or absorbing development like the phenomenon of Behaviourism arrived to consume and dominate the activities of the limited experimenting psychological community, which in this country lacked an appropriate institutional context to develop its own culture. It has been suggested that the Galtonian tradition and the emphasis on the importance of hereditary determinants saved British psychology from the extremes of American Behaviourism in the 1920s and 1930s,[169] but it is difficult to imagine the creation of any kind of movement here in the conditions of those times. British psychologists remained eclectic and independent in exchange for some of the anonymity their position caused. The experimental opportunities which had been opened up for psychological science by Darwinian theories had not been organized or exploited, while in the USA such opportunities proved less attractive than an opportunity to build research cultures around alternative theories such as those connected with Behaviourism, which were home-grown and which could benefit from the support of human and material academic resources and from traditions unfamiliar to Great Britain. 'By 1913, *Who's Who in Science* (published in England) reported the United States was the most productive nation in psychological research, with 84 of the world's leading investigators (surpassing the combined totals of Germany, England, and France). Only here, among all the sciences, was America the world's leader.'[170]

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[169]Broadhurst, P.L. (1967) *Psychology in its natural habitat. An inaugural lecture delivered in the University of Birmingham on 16 February 1967.* University of Birmingham, pp.13 & 14.
[170]Joncich, G. (1968) E.L.Thorndike: the psychologist as professional man of science. *American Psychologist*, 23: 434-46.

CHAPTER 2

THE FIRST CENTRES OF TEACHING AND RESEARCH AND THEIR ORGANIZING STAFFS

Introduction

In the editorial of the first volume of the *British Journal of Psychology* in 1904, James Ward reported that, internationally, there were 'forty laboratories for the experimental investigation of psychological questions, most of quite recent date [but] in the United Kingdom, [only] half a dozen lectureships had lately been founded in different universities to promote psychology as a science'. This modest state of affairs would remain for some time to come, since, apart from the lingering philosophical and religious hostility to psychology, much greater pressure was being exerted by the other, more established sciences for better facilities. Furthermore, animal work itself would often only be introduced long after the initial struggle to win general laboratory provision for psychology. By contrast, in the United States of America at the beginning of the century the enthusiastic adoption of the 'new psychology' was reflected in the strong shift of focus from armchair to laboratory, and from philosophy to experiment. Between 1874 and 1904, 54 psychological laboratories were established in North America; in 1904 there were four independent psychology departments in American universities, but 34 a decade later.[1] Dewsbury[2] notes that by 1910 there were eight laboratories of animal psychology in the United States and courses in the area offered at another dozen or so schools, the *Journal of Animal Behavior* being founded in 1911. By 1927 animal psychology was the subject of research in at least 40 American laboratories, while it was included additionally in the course work of 31 colleges and universities.[3]

In 1877, Ward had wanted to start a psychological laboratory at Cambridge, which would have been the first in the world, but was prevented by an idealist opposition that identified a laboratory for the study of mind with support for materialism. When with the logician Dr Venn he tried to establish experimental psychology as a distinct

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[1] Joncich, G., (1968) E.L.Thorndike: the psychologist as professional man of science. *American Psychologist*, 23: 434-46.
[2] Dewsbury, D.A. (1978) *Comparative animal behaviour*. New York: McGraw-Hill Book Co., p.22.
[3] 'The leadership of America in comparative psychology is very largely due to this extensive development of the laboratory method during the past three decades.' (Warden, C.J., 1927, The Historical Development of Comparative Psychology. *Psychological Review* XXXIV: 135-168.)

discipline, the Senate turned it down on the grounds that it would 'insult religion by putting the human soul in a pair of scales.'[4] Instead, Leipzig established the first laboratory of experimental psychology soon after. Further unsuccessful attempts were made in 1882 and 1886. Ward managed, however, to enable the American James McKeen Cattell to set up an 'unofficial' psychology laboratory at Cambridge between 1887 and 1888, unique in Britain at the time.[5] Cattell's interest in this exercise resulted from his earlier activities in Germany at Leipzig under Wilhelm Wundt.[6] The idealist reaction gave way quite soon so that psychology became established at Cambridge, London and Manchester. At Oxford the opposition persisted and greatly retarded the progress of psychology there. Meanwhile, by 1895, over two dozen psychology laboratories had been established in the United States of America.[7] Philosophical antagonism has been blamed for much of the academic neglect of psychology in Britain, which can be exemplified by the absence of a chair in Glasgow until 1955.[8] The poor climate led to a worsening of the situation as leading figures like William McDougall and C.S.Myers gave up the fight to promote psychology at Oxford and Cambridge and sought new challenges elsewhere. A lack of academic psychologists resulted in a dearth of new ideas and a failure to profit, as did the Americans, from advances made by British neurophysiologists such as Head, Sherrington and Adrian.

After it was founded in 1901, ironically the year marking the final published work in comparative psychology of L.T.Hobhouse, the last of a neglected succession of innovative experimenters partcularly inspired by Darwinian theories, the British Psychological Society had to operate against 'a background of prolonged and massive academic neglect, not untinged with hostilities.'[9] It has been claimed that Ward himself, by the time he had become joint editor of the new *British Journal of Psychology* in 1904, now 'held views unfriendly to scientific progress in psychology'

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[4]Hearnshaw, L.S. (1987) *The shaping of modern psychology*. London: Routledge & Kegan Paul, p.125.
[5]Sokal, M.M. (1972) Psychology at Victorian Cambridge - the unofficial laboratory of 1887-1888. *Proceedings of the American Philosophical Society*, vol.116, no.2, pp.145-147.
[6]Cattell wrote to his parents from Cambridge on 5 October 1887: 'I have been busied this afternoon trying to find a place for a psychological laboratory. All the buildings are very crowded. Some of the colleges are rich, but the university itself is poor, and finds it expensive to house the laboratories and museums which have grown so rapidly during the past few years. I suppose, however, we shall be able to get something. I dine with Ward tomorrow to talk it over'. Ward had earlier advised Cattell: 'It is, I fear, pretty clear that if a beginning is to be made it must be in some college ... & not in the University'. (Sokal, M.M., 1981, *An education in psychology. James McKeen Cattell's journal and letters from Germany and England, 1880-1888*. Cambridge, Massachusetts, and London: M.I.T. Press, p.281).
[7]Hearnshaw, L.S. (1987) op. cit., p.139.
[8]Hearnshaw, L.S. (1962) Sixty years of psychology. *Bulletin of the British Psychological Society*, 46, p.7.
[9]ibid., p.10.

and attempted 'to keep psychology unspotted by physiological impurities and psychometric methods'; he 'turned psychology away from empirical investigations and towards philosophical abstractions'.[10] Ward particularly disapproved of atomism,[11] and his status and influence helped to ensure that Cambridge remained largely unreceptive to it, so that the intense interest as raised shortly afterwards in the U.S.A. in the novel stimulus-response, conditioning and learning theories, was in the U.K. held back until the enthusiastic engagement of modern versions of these theories in the 1950s. Furthermore, because the study of psychology before the First World War offered no professional opportunities,[12] the intake of students was inevitably restricted. It may be that this feature of the subject area further encouraged access to it by aspiring women scientists who felt that career prospects, uncertain and socially unexpected of them in any case, were worth chancing for greater long-term rewards.

In Volume X of the *British Journal of Psychology*, W.H.R.Rivers argued the case for a retention of animal behaviour studies:

> Another branch of psychology is one which might at first sight seem even more remote from the interests of the physician than that I have just considered [ethnology]. The study of the mental processes of animals is one in which this country has had, and still has, great names, but the number of its votaries is at present so small that there does not seem to be any immediate prospect of the foundation of a Special Section [of the British Psychological Society] devoted to its study.

Rivers thought that animal psychology should have profound interest for the physician because of the importance of instinct, and from animal psychology came the chief knowledge of instinct. 'Morbid psychology has the brightest prospects, and this subject is destined to illuminate many of the dark regions in our knowledge of mental development.'[13]

Matters had improved slightly from the vocational point of view after the war's end, and in 1923 the Psychology Section of the British Association for the Advancement of Science was authorized, as revealed in its published *Reports*, to set up a committee to consider the character of a first-year university course in experimental psychology.

[10]Hearnshaw, L.S. (1964) *A short history of British psychology 1840-1940*. London: Methuen, pp.136&139.
[11]Ward, J. (1893) Modern psychology: a reflexion. *Mind*, New Series, II: 54-82.
[12]Except to Cyril Burt, who became in 1912 Britain's first professional psychologist on his educational appointment to London County Council.
[13]Rivers, W.H.R. (1919) Inaugural address to the first meeting of the Medical Section of the British Psychological Society, 15th May 1919. *British Journal of Psychology*, X, p.189.

Another committee examined and reported on the place of psychology in the medical curriculum (1928), and between 1931 and 1933 a committee enquired into the occupations for which a training in psychology was necessary or desirable, and into the place psychology should occupy in the curricula of various university degrees. Similar investigations later followed into the role of psychology as a science in adult education (1937).

Cambridge

The Cambridge laboratory and experimental psychology at Cambridge have been noted as contributing until 1940 half the history of British experimental psychology,[14] but the importance of Cambridge for the development of studies in animal behaviour during this time lies mainly in the advice given by such as Myers to workers in other centres. In 1897 Rivers was elected to the newly established lectureship in physiological and experimental psychology and set up a small laboratory in one room of the old Physiology Department. He prompted the Moral Sciences Board in 1901 to persuade the Senate to provide £35 per annum for apparatus and 'more adequate accommodation for experimental psychology.'[15] The new accommodation was in a little building in St. Tibbs Row, and was very soon being described as dismal. It is, however, surprising that the accommodation was regularly upgraded during these years, and that James Ward, himself not an experimenting psychologist, had managed to obtain in 1891 a cash grant of £50 for psychological apparatus.[16] Rivers's earlier appointment in 1893 as Lecturer in Experimental Psychology and the Physiology of the Senses had been described by one member of the Senate as a 'ridiculous superfluity'. At the time of Rivers's second appointment in 1897, Ward also became Professor of Moral Philosophy, and as a result of his efforts, and with the support of the physiologist Sir Michael Foster, whose liberal views were meanwhile an effective contribution to the 'revolution of the dons' at Cambridge, Ward had secured for Rivers his first laboratory that year.

In 1902, Myers, a former student of his, arrived to work as Rivers's assistant. He became Demonstrator in 1904, declining an offer of the salaried secretaryship of the

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[14] Boring, E.G. (1950) *A history of experimental psychology*. 2nd ed. New York: Appleton-Century-Crofts, p.488.
[15] Boring, E.G. (1950) ibid., p.490.
[16] Myers, C.S. (1936) Charles Samuel Myers. In: Murchison, C.A. (ed.) (1936) *A history of psychology in autobiography*. Vol.III. Worcester, Mass.: Clark University Press and (1961) New York: Russell & Russell, p.217.

British Association for the Advancement of Science[17] (and helped to found that year the *British Journal of Psychology*, which he edited between 1911 and 1924, and which in 1914 became the organ of the British Psychological Society). In the following year a recurring annual grant of £50 for apparatus and expenses was awarded, as well as a 'decent small cottage' as improved accommodation on the River Cam at 16 Mill Lane, belonging to the University Press and recently used by the Department of Surgery. The annual grant remained at the same level until 1916, but by 1909 the cottage itself was being referred to as 'damp, dark and ill-ventilated', and later reverted to the Press. Sir Frederic Bartlett later said of it: 'It is a wonder Behaviourism did not first grow there instead of later and elsewhere ... rats abounded. Anybody could observe startle reflexes firing off in all directions.'[18] In 1907, the Special Board for Moral Sciences had asked the Senate to provide better accommodation once more, since there were then at Mill Lane fourteen undergraduates, two advanced students and three research graduates, twice as many as the laboratory should have held. In December 1908 the Cambridge University Association launched an appeal to finance better premises, and in the following year, when Rivers resigned from the psychological element of his lectureship, Myers became the first lecturer whose duties were solely confined to experimental psychology. He later said of Rivers: 'Few could realize, so fully as I, all that he had done to promote the scientific status and recognition of the subject in Great Britain.'[19]

At the time of the launch of the appeal in 1908, the Cambridge University Association issued a confidential 'Statement of the case for the establishment of a laboratory for experimental psychology'.[20] This began by noting, firstly, the well established recognition given to psychological sciences by universities in the USA and continental Europe, in the form of special buildings for teaching and research; and, secondly, laboratory provision and special lectureships in Oxford, London, Liverpool, Edinburgh and Glasgow. Many examples were offered of areas of experimental interest reinforcing psychology's scientific standing and importance for society, including 'the mental characters of normal and defective children, primitive peoples and animals'. An effective contrast was made with the inadequate nature of the temporary accommodation at Mill Lane, which could not cope with the increasing number of students and whose land would soon be required for the extension of the University

[17]Myers, C.S. (1936) ibid., p.219.
[18]Bartlett, F.C. (1937) Cambridge, England 1887-1937. *American Journal of Psychology*, 50: 97-110; Zangwill, O.L. (1954) *Psychology as the study of behaviour*. Cambridge: University Press, p.19.
[19]Myers, C.S. (1936) op. cit., p.228.
[20]Cambridge Univ Lib MS Room: Prem. VII. 4.

Press buildings. It was estimated that at least £4,000 would be needed to build the laboratory and classrooms, with more to cover maintenance, equipment and other expenses, the contribution of the University being limited to the allocation of a new site because 'owing to the present demands on its income the University will for a long time be incapable of defraying the cost of building'.

As a student, Myers had developed a strong interest in anthropology and experimental psychology (and, temporarily, in pathology), and, like William McDougall, qualified in medicine with no real intention to practise it. Myers was well prepared to make good use of his new responsibilities. From 1906 he had had a part-time appointment as Professor of Psychology at King's College, London until 1909, when he published his practical *Textbook of experimental psychology*. His *Introduction to experimental psychology* appeared in 1911 'with the object of informing the general public concerning the scope of psychological experiment.'[21] The appeal launched in 1908 successfully guaranteed money, much of it his own and that of his relatives, to build a new laboratory as an independently administered wing of the new physiological laboratory funded by the Draper's Company. The Senate gave its approval for building to begin in 1910, but not until objections had been expressed about the validity of psychological experimentation. Dr Mayo announced to the Council of the Senate that on principle he 'objected very strongly indeed to the grant of one single penny to Experimental Psychology' because experimental psychology was not possible.[22] The foundation stone was then laid in 1911 and the premises opened two years later: '... the new laboratory ... I had planned after holiday visits to American and German universities. It contained on three floors a lecture room, mechanic's room, animal room, library, experimental classrooms, dark-room, sound-proof room, and research rooms ... It remains, I think, the finest psychological laboratory in Great Britain and one of the best planned of any elsewhere.'[23] A similar physical description of the laboratory building had been given earlier by Bartlett in the *Cambridge Review* of 7th November 1912. In a speech to mark the opening of the laboratory, Myers looked to the future of psychology at Cambridge as a discipline connected with physiology and having great potential for being applied in the field, resulting (partly) from its relations with biology, the study of animal behaviour, and education. An open day was held on 9th June 1914, at which demonstrations included the discrimination of light and sound resulting from the individual and inherited mental differences of guinea pigs, and the

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[21] Myers, C.S. (1936) op. cit., p.220.
[22] See the Cambridge *Reporter*, vol. 40, p.361.
[23] Myers, C.S. (1936) op. cit., p.221.

use of a maze to demonstrate animal learning, the extent of persistence after rest, reversal training, spontaneous learning of short cuts, etc.

During rebuilding for the new animal house and demonstration theatre for the Department of Psychology in 1971 a canister was discovered under the foundation stone of the laboratory, containing a variety of documents dating from 1908 and 1911. These included the confidential statement described above, an appeal for funds to equip the laboratory and a list of subscribers to the building fund. Copies were made before the original material was replaced, together with further material from 1971.[24] The cost of the building had eventually worked out at £3,700, and 32 subscribers donated £3783.4s.0d. Apart from his own anonymous donation of £3,000, Charles Myers and his family openly contributed £400. Others named included the psychologists E.M.Smith, G.Dawes Hicks and W.H.R.Rivers, and the majority of the remainder represented benefactors whose names suggested continental and Jewish origins, most probably business acquaintances and friends of the Myers family. The Cambridge University Association supplied extra funds to meet overheads such as architect's fees, clerk of works's salary and fittings, while seven private donors (once more, a mixture of academics and business people) provided £53.2s.0d towards equipment such as tables, cupboards, benches, lighting and telephones.

The proximity of the Psychology Laboratory to the Department of Physiology had been quite deliberately engineered by Myers and Rivers to further intellectual relationship between the two disciplines.[25] The layout of the new laboratories had been planned with flexibility and foresight, and Myers was rewarded with the title of Director, although this did not involve any financial advantage. He acquired for his staff an assistant and a workshop mechanic, and enjoyed the help of G.Dawes Hicks, Cyril Burt and occasionally Rivers. In 1914 he became Reader in Experimental Psychology before activities were suspended during the war. On returning to Cambridge after hostilities had ended, and with the practical value of psychology established, for example, in the treatment of victims of shell-shock, Myers found that applied psychology was outstripping its academic parent,[26] since senior university staff were unwilling to entertain extra versatility for experimental psychology. He recalled:

> On demobilization I returned to Cambridge, fired with the desire to apply psychology to medicine, industry, and education and becoming

[24] Cambridge Univ Lib MS Room. Prem. VII. 4.
[25] Zangwill, O.L. (1977) Obituary: G.C.Grindley (1903-1976). *Quarterly Journal of Experimental Psychology*, 29: 1-3.
[26] Boring, E.G. (1950) op. cit., p.493.

> increasingly disgusted, after my very practical experience during the War, with the old academic atmosphere of conservatism and opposition to psychology. I found that the wild rise of psychoanalysis had estranged the Regius Professor of Physic; I received little encouragement from the Professor of Physiology; and the Professor of Mental Philosophy, to my surprise, publicly opposed ... 'experimental' ... in the title ... of Reader in Experimental Psychology. Thus medicine, physiology, and philosophy had little use then at Cambridge for the experimental psychologist.[27]

He eventually left to devote his talents to industrial psychology in 1922, being succeeded in the Readership by his assistant and pupil, F.C.Bartlett. Looking back at Myers's influence on psychology at Cambridge, Zangwill felt that he had not promoted it sufficiently as a biological science: for example, his *Textbook* followed German psychophysical tradition, which had little in common with the evolutionary outlook of British biology, and no reference was made to experiments on animal intelligence.[28] Indeed, although Myers was largely responsible in 1919 for the re-organization of the British Psychological Society into specialist sections, none of these was based on comparative or animal psychology.

F.C.Bartlett, who had come to Cambridge in 1909 and later succeeded Myers, continued to consolidate the laboratory, which in 1926 became recognized as part of the Biological Sciences Faculty. He tried hard that year, as Chairman of the Board of Psychological Studies, to convince the University Appointments Committee of the overdue need to create a professorship and improve staffing levels to six lectureships, referring to the case made about staffing to the Royal Commissioners in 1924 and the intervening increase in students, in the variety of their interests, in research activity, and in psychology's relevance to other areas such as medicine: better staffing was necessary to maintain the conditions laid down in the New Statutes. Bartlett continued:

> At present the Reader in Experimental Psychology gives 112 hours of lectures in the year; the University Lecturer in Psychopathology 78 hours of lectures; the Demonstrator in Experimental Psychology 32 hours of lectures and 160 hours practical class work. The Department is full to its utmost capacity of research students. The peculiar position of psychology as a 'border-line' science with interests in many different directions renders its teaching necessarily very diversified and arduous.[29]

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[27]Myers, C.S. (1936) op. cit., pp.224-5.
[28]Zangwill, O.L. (1954) op. cit., p.22.
[29]Cambridge Univ. Lib. MS Room. Comm.B.7.6.iii.

Bartlett had been drawn to study at Cambridge 'largely because Rivers was there and my interests were turning strongly towards anthropology,'[30] whereupon his involvement in experimental activity began to be developed under Myers. He arrived in 1909 with a first in philosophy from London. Subsequently, his training 'linked psychology to philosophy, to medicine, and to anthropology while emphasizing laboratory experiment on behaviour'. He neglected animal studies and physiological psychology: 'his thinking drew little from an evolutionary source, and placed no emphasis on the structure of the brain', although like W.H.Thorpe, a near contemporary, he suffered illness in childhood that kept him from school and resulted in much exploration of the rural environment around his parents' home, a circumstance that in Thorpe's case proved influential.[31] It was not until 1931 that Bartlett was elected to the first professorship in experimental psychology, and in 1933 he recruited G.C.Grindley, an animal psychologist, who had come to Cambridge from Bristol in 1928 as an acting demonstrator. Grindley was quick to take advantage of the proximity of the Psychology Laboratory to the Department of Physiology. The position of demonstrator was soon promoted in 1936 to that of the third full lecturer in the laboratory, a position which Grindley was to hold for over thirty years.

Since the First World War the Medical Research Council had encouraged the development of Cambridge research and provided assistance to many students who later became staff of other universities. This created further pressure on working space in the laboratory opened in 1913 on the Downing site.[32] By 1935 the shortage of space necessitated an overflow into available rooms in the Physiology and Pathology Departments, but it was clear that the good planning of the 1913 building, resulting from Myers's holiday visits to the American and German universities, had envisaged possible extensions to its south face. At the time Bartlett reported that these were

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[30]Bartlett, F.C. (1936) Frederic Charles Bartlett. In: Murchison, C.A. (ed.) (1936) *A history of psychology in autobiography*. Vol.III. Worcester, Mass.: Clark University Press and (1961) New York: Russell & Russell, p.39.

[31]Broadbent, D.E. (1970) Frederic Charles Bartlett 1886-1969. *Biographical Memoirs of Fellows of the Royal Society of London*. Vol.16, pp.1, 2 & 8. Colin Crampton asserts that Bartlett was an 'empire builder' who was concerned to place pupils with interests and beliefs similar to his own in influential positions (Crampton, C. (1978) *The Cambridge School. The life, work and influence of James Ward, W.H.R.Rivers, C.S.Myers and Sir Frederic Bartlett.* Edinburgh University: unpublished Ph.D. thesis). Although his wife had played a key role in the inauguration of laboratory studies in animal psychology, her work drew to a close soon after their marriage. G.C.Grindley did not progress beyond his lecturereship at Cambridge. Of those of his many other pupils and assistants who went on to run departments of psychology elsewhere, only G.C.Drew had specific interests in animal psychology. Crampton is therefore probably right to imply that the institutionalization of British animal psychology 'lost out' in Bartlett's ambitious manoeuvres.

[32]Zangwill, O.L. (1962) The Cambridge Psychological Laboratory. *Bulletin of the British Psychological Society*, 48, p.22.

effected in 1937 and provided twelve additional research rooms and a modern workshop.[33] Finally a summary of Cambridge work is given by K.J.W.Craik, director of the Medical Research Council Applied Psychology Research Unit, founded in Bartlett's department in 1944, who reflected that in peace time the Cambridge Pyschological Laboratory had been largely concerned with work on human and animal learning, and on visual and auditory perception, mainly by the study of these senses in human subjects, but sometimes aided by electrical recording of nerve impulses in animals and by other physiological methods.[34]

Since animal experimentation at Cambridge had failed to become established at the level of intensity achieved in many American universities, Bartlett was inclined to compare the academic and experimental contexts as they had developed either side of the Atlantic in the first half of the twentieth century. As in the cases of Ward, Rivers and Myers before him, Bartlett's influence had played its part in creating the British context. He was critical of the all-embracing theories proposed by the behaviourists and of their enormous superstructure of systematic belief. Meanwhile, the experimental strategies adopted for animal learning and behaviour studies in the USA 'might almost as well have been planned in the early 1900s'.[35] He had said, in addressing American psychologists:

> Everywhere I went [in the USA] I was impressed by tremendous activity and frequently by beautiful technique. The instrumentation is in general far beyond anything that British psychologists can anywhere at present achieve, even where the skill and the will are available. I hope it will not appear ungracious if I say that I am less sure about the ideas. It seemed to me that sometimes brilliant instrumentation was mistaken for well directed experiment. Speaking very generally, I think that problems are still being developed along the old, conventional lines, and that the methods still remain little different from those of years which to some of us seem to belong to the far past. I fancy that in England in particular we have had more of a rough jolt out of the old ruts, and are searching, though perhaps with little success, for methods which will

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[33]Bartlett, F.C. (1937) op. cit. This account of the improvements given in the *American Journal of Psychology* was actually premature, as the minutes of the meetings of the Psychological Laboratory Extension Building Committee (on which Bartlett and Grindley served) show that although on 19 January 1938 Bartlett advised at least twelve research rooms, a workshop and an animal room with thermostatically controlled, quiet heating and sound insulation, on 5 May the approved, cheaper scheme allowed only for ten research rooms, rather than twelve with the additional workshop and animal room. The work was then scheduled for completion by January 1939. (Cambridge Univ. Lib. MS Room. Prem. vii. 25.)

[34]Craik, K.J.W. (1945) The present position of psychological research in Britain. *British Medical Bulletin*, 3: 24-6.

[35]Bartlett, F.C. (1955) Fifty years of psychology. *Occupational Psychology*, 29, 4: 203-16.

> retain that accuracy of control which scientific research demands, but will at the same time bring us into more immediate contact with behaviour beyond the laboratory.[36]

Twenty years before, in 1927, he had said of John Watson's *Behaviourism*: 'It signalled a great fall. The last remnants of caution have disappeared'.[37] He had at first respected Watson's animal work as relevant to studies of human psychology, but as Bartlett then came to form his long-term opinion of behaviourism as over-ambitious dogma, animal psychology began to suffer through its association with the behaviourists and atomists. These thoughts seemed to echo the criticism of Thorndike by Hobhouse and to revive the argument for better experimental theory and design to match and make proper use of sophisticated procedure. As before, the problem that procedure could become accepted as an end in itself was real enough.

Oxford

Oxford had no psychological laboratory until 1936, when William Brown became Director of the Institute of Experimental Psychology; and no chair in psychology until 1947. However, and on an unofficial basis as Wilde Reader in Mental Philosophy between 1904 and 1914, William McDougall had managed to use the laboratories of Sherrington and his fellow physiologist Gotch, Professor of Physiology.[38] This caused much trouble and hostility, and Wilde himself attempted to remove McDougall. In a letter to Lloyd Morgan, McDougall,[39] while looking forward to later 'instructive criticism' of his work, thanks him for his congratulations on his election to fellowship of the Royal Society. McDougall says that such an election was proof of the recognition of psychology by the Royal Society, a valuable step in the direction of academic professionalization for the subject. However, soon after the First World War

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[36]Bartlett, F.C. (1947) Visitor to America. *American Psychologist*, 2: 372-4.
[37]Bartlett, F.C. (1927) Critical notice. 'Behaviourism' by John B.Watson. London: Kegan Paul Trench, Trubner & Co. Ltd. 1925. *Mind*, 36: 77-83.
[38]Gotch's receptiveness to students of psychology as well as his belief (unusual for the UK and like that of Edward Thorndike in the USA) in the links between experimental psychology and education are revealed in the evidence he gave to the Royal Commission on Vivisection on 30 October 1907. Students of philosophy and psychology asked to come specially to the last course of [physiological] lectures on the central nervous system, and he said that 'in a special annex to my department which is now being built, special rooms are reserved for this particular subject, psycho-physics, which is taken up, not only by philosophers, but by those who are qualifying for the education scheme of the University ... All education should be based on neurology'. Royal Commission on Vivisection. Appendix to 4th Report of the Commissioners. Minutes of Evidence 13638-13639, October - December 1907. HMSO 1908. (WIHM CMAC: SA/RDS H.14/22.)
[39]McDougall, W. (1912) Letter to C.Lloyd Morgan, 2 March 1912. Bristol University History Collection: DM 128/256.

McDougall was lost to the USA. In his autobiography[40] he explains the early and lasting motivations in his work, which could have resulted in a contribution to domestic rather than American developments in studies of animal behaviour had he not emigrated: 'I was ambitious; but I looked down on all money-making vocations. All trade and business I regarded with mild contempt; and even the earning of a large income by the practice of law or medicine seemed to me unworthy of a free man'. In the 1890s he had studied medicine as a vehicle for a wide range of interests connected with psychology, but 'I saw how difficult it is to follow medicine as a profession and to maintain at the same time an active interest in research; and I was all for research'.

McDougall therefore decided to study under G.E.Muller at Göttingen whom he regarded as the leading exponent, in the last years of the century, of exact laboratory methods in psychology. James Sully invited him to introduce these methods at University College, London in 1900, where in his laboratory he and a few others inaugurated the British Psychological Society. At Oxford he published his *Social Psychology* (1908), in which he argued that behaviour resulted from instincts, which could be modified as a result of experience. But rather than explain these instincts, he catalogued them. This 'nominal fallacy' meant that 'it was probably he more than anyone else who led psychologists to be highly skeptical of the usefulness of the instinct concept - an orientation that was to be of great importance when psychologists and ethologists began interacting nearly half a century later.'[41] Having become established at Oxford he subsequently wrote:[42] 'I had a secure and comfortable position at Oxford in which I could live out my working years; and after the War there was a marked increase of interest in psychology; my regular lectures now had some two hundred hearers ... However it had always been my principle to accept whatever challenge life might bring. Harvard would be a stimulating adventure; whereas at Oxford I might too easily subside into inactivity'. In America he was able to develop his experimental interests and began to test, long term, the Lamarckian theory of the inheritance of acquired characteristics by using for the first time laboratory-based behavioural studies of successive generations of specially trained rats. This work attracted comment and replication by Hazlitt and Crew[43] in England, but they believed

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[40]McDougall, W. (1930) William McDougall. In: Murchison, C.A. (ed.) (1936) *A history of psychology in autobiography*. Vol. I. Worcester, Mass.: Clark University Press and (1961) New York: Russell & Russell.
[41]Dewsbury, D.A. (1978) *Comparative animal behaviour*. New York: McGraw-Hill Book Co., p.11.
[42]McDougall, W. (1930) op. cit.
[43]Crew, F.A.E. (1936) A repetition of McDougall's Lamarckian experiment. *Journal of Genetics*, 33: 61-101. At the Institue of Animal Genetics of the University of Edinburgh Crew trained 18 generations of rats in a water tank, using six trials a day to a criterion of 12 'correct' shock avoidances. His experimental design and control appeared superior, and to disprove McDougall's

that this attempt to deal a blow to the 'mechanistic biology' or behaviourism prevalent in the USA of the 1920s was, however worthy, inconclusive. McDougall's obsession with this exercise did him little good at Harvard, and he soon transferred to Duke University in North Carolina. His rejection of contemporary trends in American experimental psychology were sustained by his obdurate character but led to ostracization. In his review of the development of comparative psychology in 1927, Warden dismissed McDougall in a couple of lines as one whose theories did not need to be discussed in detail.[44]

Just as in England he had been critical of neo-Darwinism, so in his new surroundings his independent spirit had given him the confidence to attack a movement in psychology in which there was some national pride of ownership. He described the term 'Behaviorist' as barbarous[45] and his tendency to Lamarckism matched a preference for concepts of instinct, conation and purposive behaviour which hinted at later ethology and cognitive psychology. But in the 1930s he had become 'a symbol of what American psychology had most set itself against'.[46] In 1934 he was still corresponding with Lloyd Morgan, and welcomed his criticism of his published studies, acknowledging that such criticism helped to promote psychology. Being especially familiar with attitudes to scientific psychology on both sides of the Atlantic, he also complained of the pre-occupation with experimental procedure at the expense of theory in a letter he sent in 1934 to Lloyd Morgan, who died that year: 'There are too many workers in our field wholly absorbed in small detail and too few seriously concerned with the general principles of larger problems.'[47]

Oxford was the venue for the first International Congress in Psychology in 1923, organized by C.S.Myers who was elected its president and who had recently cut his professional ties with Cambridge. This event did much to rebuild international links in the subject after the First World War,[48] but at Oxford itself little happened in psychology for over a decade. When the Institute of Experimental Psychology was constituted in May 1936, William Stephenson was appointed Assistant Director and

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claims for the Lamarckian hypothesis.
[44]Warden, C.J. (1927) The historical development of comparative psychology. *Psychological Review*, XXXIV: 154-155.
[45]McDougall, W. (1930) A second report on a Lamarckian experiment. *British Journal of Psychology*, 20: 201-18.
[46]Heidbreder, E. (1939) William McDougall and social psychology. *Journal of Abnormal and Social Psychology*, 34: 150-60. Cited by Webb, W.B. (1989) William McDougall's Lamarckian experiments. *The Psychological Record*, 39: 159-76.
[47]McDougall, W. (1934) Letter to C.Lloyd Morgan, 24 July 1934. Bristol University History Collection: DM 128/537.
[48]Myers, C.S. (1936) op. cit., pp. 228-9.

St. Giles School at 34 Banbury Road adopted as accommodation for graduate teaching and research. There was a large laboratory with dark room, a lecture room, office and research room. A small workshop was provided with apparatus grant-aided by the Rockefeller Foundation.

Between 1935 and 1940, S. Zuckerman, Demonstrator in Anatomy, organized a number of biologists to undertake work on the behaviour of animals, especially primates, but this psychological activity took place beyond the Institute[49] at London Zoo, where Zuckerman had been employed as Prosector by the Zoological Society of London in 1928. He arrived in Oxford in 1934, and found that because of his experience in American behavioural laboratories and his published work on the social behaviour of monkeys and apes, he was enabled by the University, after encouragement from students, to develop animal behaviour research there. This began with an experiment to confirm that monkeys cannot make numerical abstractions, when Bertrand Russell (former tutee of Douglas Spalding) was consulted for advice. Of more practical applied value might have been the results of another experiment which Zuckerman had intended to undertake in the 1930s to compare the learning ability of human 'mongoloids' and baboons, but this plan was abandoned lest news of it were to stimulate hostile comment.[50] In 1936 Zuckerman and others, including Julian Huxley as president and James Fisher, the ornithologist, as secretary, inaugurated the Institute of Animal Behaviour, whose first bulletin, edited by Zuckerman, was printed in Oxford in 1938: 'I got the idea that, in order to stimulate a wider interest in the subject, what we needed in the United Kingdom was a national society or institute for the study of the subject'.[51]

London

In London Sully, with the support of Lubbock, Galton and others, persuaded University College to establish a small laboratory for experimental psychology in 1897, the first of its kind in England. It was to begin with housed in a small room that also served as a library store.[52] Rivers from Cambridge was used as a consultant in its

[49]Oldfield, R.C. (1950) Psychology in Oxford 1898-1949, Parts 1 & 2. *Bulletin of the British Psychological Society*, 1: 345-53 & 382-7.
[50]Zuckerman, S. (1978) *From apes to warlords: an autobiography 1904-46*. London: Hamish Hamilton, p.47.
[51]Zuckerman, S. (1978) ibid., p.99.
[52]Harte, N. and North, J. (1990) *The World of University College London 1828 - 1990*. London: University Press.

running, and it was equipped with apparatus belonging to Hugo Munsterberg, which had been left behind at his Freiburg laboratory on his emigration to the United States of America.[53] McDougall carried out some psychophysiological experiments there until his departure for Oxford. A small laboratory was also established in 1903 at King's College by C.S.Myers, who from 1906 became part-time Professor of Psychology. Carveth Read succeeded Sully at University College in 1903 and developed an interest in animal behaviour, on which he concentrated when he retired from his chair in 1911 to become Lecturer in Comparative Psychology until 1921.[54] He soon began to waive his share of the student - sourced fees that supplemented his lecturer's salary, and he frequently made single donations in the hope that the laboratory would benefit, although the College Committee added these contributions to the general Psychology grant and Carveth Read in due course made more specific (but unrealized) proposals for the development of a special laboratory for animal psychology. On his retirement and becoming Emeritus Professor of Philosophy and Comparative Psychology, his donations to support the existing laboratory continued.[55] In the meantime, in 1907, the laboratory had been rehoused on the second floor of the building recently vacated by University College School.[56] Carveth Read had not been well able to tackle the technical aspects that practical research presented, although he had turned to Lloyd Morgan for advice.[57] An attempt to carry out a maze-learning experiment with goldfish had to be abandoned because of the catastrophic death-rate,

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[53]Staff (1897) Psychological laboratory at University College, London. *Mind*, 6: 448.

[54]In his letter of resignation, on grounds of increasing age, he drew the attention of the College Committee to anomalies in the division of the teaching of psychology between the Grote Professor of the Philosophy of Mind and Logic and the Reader of Experimental Psychology. Univ Lond, UC MS Lib. Minutes of College Committee. Item 38, 6 December 1910.

[55]Univ Lond, UC MS Lib. Minutes of College Committee. Item 123C, 1 May 1917; Item 249, 1 July 1919; Item 249E, 7 June 1921.

[56]Hale Bellot, H. (1929) *University College, London 1826-1926*. London: University of London Press, p.409.

[57]An inspection of the University College Calendars (sessions 1912-1921, London: Taylor and Francis) suggests that Carveth Read's undergraduate lectures on comparative psychology did not include any practical experimental work. (Archives of University College London, held in the Central Records Office.) He wrote to Lloyd Morgan in 1912: 'You were kind enough to say some time ago, that if difficulties arose in Comparative Psychology I might consult you ... Can you tell me where to find information about the attraction that light has for moths and fishes? From experiments made last summer, I inferred that the tendency of moths to fly to more or less luminous spaces and the tendency to fly to a point of bright light are distinct, and also vary in different species. Is anything known as to the different effects of light upon different species of fishes? For here again it may be possible to distinguish between useful phototropism and the fascination of a bright flare, as used by some fishermen to attract fish within spearing distance. Similarly with birds and lighthouses, etc. ... Lectures here on Comparative Psychology have begun pretty well; but there is little chance of establishing a laboratory at present for want of facilities for keeping animals. However with long holidays some work may be done in the country'. (Read, C., 1912, Letter to C.Lloyd Morgan, 1 January 1912. Bristol University History Collection: DM 128/251.) Conducting work both in the laboratory and in natural conditions would have been a policy acceptable to Lloyd Morgan as also later to Tinbergen after the Second World War.

and this was the first and last attempt at animal experiment wholly carried out within the Department until 1950.[58]

Carveth Read's proposals for an animal laboratory were not echoed in the report given by his successor, Charles Spearman, to the Meeting of Science Members of the Professorial Board on 28 March 1919, when the post-war requirements of the Department of Psychology were addressed.[59] Just as in 1926 the Cambridge laboratory had been gathered into the biological sciences faculty, so co-operation with departments in the biological and medical sciences began to be discussed at University College early in 1927, when Spearman, together with the professors of anatomy, physiology and zoology and the reader in cultural anthropology, submitted a report recommending linked development of accommodation, equipment and experimental staff reflecting considerable disciplinary cross-over between 'a natural and closely inter-related group of subjects' (including pharmacology) and a biological approach to experimental psychology.[60] In 1928 the Department of Philosophy and Psychology which had been constituted in 1911 was split under, respectively, the Grote Professor of Mind and Logic and the Professor of Psychology (a new post for Spearman), and in the following year the laboratory spaces were enlarged, on the occasion of the closure of the Department of Hygiene.

In 1925, a contribution was made in the *British Journal of Psychology* by F.Aveling and R.J.S.McDowall (from the Psychological and Physiological Laboratories, King's College London), assisted by R.C.McCarthy and Miss Honoria Wells, entitled 'A note on the psychogalvanic reactions of anaesthetized cats', recounting an experiment whose purpose was further to determine by invasive means the significance for psychology of psychogalvanic reflexes.[61] Aveling was head of the Department of

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[58]Flugel, J.C. (1954) A hundred years or so of psychology at University College, London. *Bulletin of the British Psychological Society*, 23: 21-31.
[59]Univ Lond, UC MS Lib. UCL Hist: VI A/2.
[60]Univ Lond, Archives of UCL, held in the Central Records Office. Minutes of University College Committee, 1 February 1927, Appendix 3: Proposal to make fuller provision for research and teaching in psychology and anthropology, and to integrate such developments with the scheme of co-operation of anatomy, physiology, biochemistry and zoology. It was stated: 'The work of the Department of Anatomy at present includes the investigation of the brain and sense-organs and the comparative anatomy and physiology of the nervous system (for undergraduate and graduate students in Psychology). The work of the Department of Physiology includes the study of the functions of the sense-organs and the phenomena of the central nervous system, and the investigations of other problems that have a direct bearing on Psychology, and a considerable amount of work is being done in that Department which is virtually Experimental Psychology. The work of the Department of Zoology includes within its scope not only the problems of the evolution of the nervous system but also the study of animal behaviour, in other words Comparative Psychology'.
[61]Aveling, F. et al. (1925) A note on the 'psychogalvanic' reactions of anaesthetized cats. *British Journal of Psychology*, XVI: 50ff.

Psychology, King's College, between 1919 and 1931 and its professor from 1931 to 1941, but this was the only animal research he undertook.

At the time of the creation of the laboratory at University College in 1897, Beatrice Edgell was appointed to teach philosophy and psychology at Bedford College for Women as head of the department of philosophy, and she soon introduced experimental work,[62] later to become Curator of the University's Physiological Laboratory between 1904 and 1913,[63] Reader in Psychology in 1913 and Professor of Psychology in 1927. New buildings in Regent's Park were opened in 1913 by Queen Mary, and the work of the psychologists was inspected during the royal visit. 'The newly formed O.T.C. of the University of London formed an escort. The Department of Psychology, where research on the memory of rats was in progress, was especially interesting to Her Majesty.'[64]

However, Beatrice Edgell's ambitions for the experimental work of her department were not ultimately met, and within a decade she appeared to have become resigned to this. In December 1923 she reported to Council on the needs for the future development of psychology at Bedford College for Women:

> I regard preparation for the University degrees in Arts and Science as the central thread of our work and in all future developments efficiency in this respect would stand first.
>
> For the development of our special work I look to its applications in the social problems of child life and adolescence, and to its relations with Comparative Psychology.
>
> Three years ago we dropped our attempts to carry on a first hand study of Comparative Psychology. The time and effort which it required without trained assistance and special accommodation seemed disproportionate when taken in relation to other claims. To develop such study would be expensive, involving a trained attendant and the erection of an animal house. It is, however, a development of psychology which our situation in the Park renders suitable and one for which I had hoped the roof of the North Block would provide the site necessary for the animal house.

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62 Hearnshaw, L.S. (1964) op. cit., p.175.

63 E.H.Starling, Professor of Physiology at University College, remarked on 20 December 1906 that Pavlov's work 'opened up a huge vista of further operations', but such work was not taken on in the laboratory by any of the London psychologists. Royal Commission on Vivisection. Appendix to 1st Report of the Commissioners. Minutes of Evidence 4232, October - December 1906. London: HMSO 1907. WIHM CMAC SA/RDS H.14/22.

64 Tuke, M.J. (1939) *A history of Bedford College for Women, 1849-1937*. Oxford: University Press, p.216.

> I do not wish to press for this development at the present time. The general needs of the department which I have stated first constitute a prior need. Nevertheless I hope that the Council will bear this special development in mind when they have under consideration any replanning or extension of existing departments.[65]

The response of the Council at its next meetings was only to note these comments,[66] and it would appear that they took no further steps to act on them. Molly Harrower, a student of Beatrice Edgell between 1926 and 1928, and then, as a lecturer in psychology, a colleague of hers in the final year of her office in 1932-3, confirms that during those times there was no interest in the problems of animal behaviour.[67]

Aberdeen

When James McIntyre took over from Stout the Anderson Lectureship in Comparative Psychology at Aberdeen in 1899, he introduced experimental work to the lecturing programme and asked Lloyd Morgan to be prepared to advise him if necessary.[68] He pressed for a laboratory and apparatus and this was forthcoming. After thirty years and on his death in 1929 he was succeeded by Rex Knight. Rooms and a laboratory were held from 1906 in Marischal College, and at Aberdeen there had been none of the religious and philosophical opposition to the development of the study of psychology that (according to Knight)[69] hindered so many universities. Work on animal learning was begun in 1932. In sectional transactions of the British Association for the Advancement of Science in York that year, Knight reported that 'recent experiments in the training of animals, carried out in the Department of Comparative Psychology in Aberdeen University, showed once again how comprehensive trial-and-error is in animal behaviour, how large a part is played by conditioned reflexes, how adequate is the Pavlovian thesis, and how easily animals can acquire an entirely undeserved reputation for intelligence and other mental characteristics.'[70] This belittling of the mental abilities of animals provoked objections, and in the course of a published

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[65] Edgell, B. (1923, 8th December) Report to Council on the needs for the future development of Psychology. RHUL Archives, AR 334/10/1.
[66] Minutes of meetings of Council. RHUL Archives, AR 334/10/1.
[67] Harrower, M. (1996, 14th August) Personal communication.
[68] McIntyre, J.L. (1901) Letter to C.Lloyd Morgan, 31 January. Bristol University History Collection: DM 612.
[69] Knight, A.R. (1962) The Department of Psychology in the University of Aberdeen. *Bulletin of the British Psychological Society*, 47: 3-11.
[70] Knight, A.R. (1932a) How animals behave. *British Association for the Advancement of Science: Reports*, Sectional Transactions - J, 378.

response in *Nature* later in the year, Knight again referred to the work of his department in Aberdeen. It had made careful observations of animal learning under controlled experimental conditions, for example the behaviour of cats in puzzle boxes of the kind used by Thorndike.[71] Three decades after he had counselled McIntyre, Lloyd Morgan remained in touch with activities at Aberdeen, and Knight[72] wrote to thank him for his letter concerning this article in *Nature*.

Other centres

In 1919, Manchester created the first full-time chair in psychology alone, but little animal work was undertaken, an example being the study of social behaviour of domestic fowl under visiting Professor D.Katz.[73] At Liverpool, W.G.Smith had been appointed in 1905 as a lecturer in psychology to assist Sherrington in his courses on psychophysiology, but a year later departed to start the George Combe Laboratory in Edinburgh.[74] Here he managed to equip it to Cambridge standards, and his successor, James Drever, consolidated experimental work, achieving professorial rank in 1931. H.J.Watt also worked under Sherrington and then took up the new lectureship in psychology at Glasgow in 1907. St Andrews did not appoint a lecturer in experimental psychology until 1924. Meanwhile the departure of Sherrington and others caused a prolonged decline in psychology at Liverpool. A.W.Wolters at Reading was given in 1910 a 'very foul attic', a grant of £25 and £10 per annum, but he developed a good laboratory, and a proper psychology department materialized in 1920. The obituary notice of Joseph Brough, Professor of Philosophy at Aberystwyth since 1883, reported that he favoured experimental psychology. He retired in 1911 and 'before then he had succeeded in getting together the material and apparatus necessary for laboratory courses in this subject'. He promoted these courses as part of a university curriculum in 1923 in an article entitled 'The Vogue of Psychology' published in *The Welsh Outlook*.[75]

By the time of the Second World War nearly every university in Britain had a psychology department, most carrying out experiments and some enjoying the support

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[71] Knight, A.R. (1932b) The explanation of animal behaviour. *Nature*, 130: 649-51.
[72] Knight, A.R. (1932c) Letter to C.Lloyd Morgan, 14 November. Bristol University History Collection: DM 612.
[73] Pear, T.H. (1955) The Manchester University Department of Psychology, (a) 1909-1951. *Bulletin of the British Psychological Society*, 26: 21-30.
[74] Hearnshaw, L.S. (1962) op. cit., p.2.
[75] Edgell, B. (1926) Obituary notice: Joseph Brough. *British Journal of Psychology*, XVI, p.363.

of the Medical Research Council and the Royal Society.[76] The accelerative effect on the development of psychological facilities caused by the Second World War was a reflection of that of the First.[77] But among the universities that failed paradoxically to set up a psychology department or laboratory until after the war was Bristol, where Lloyd Morgan as both Principal and Professor, at first of Geology and Zoology and later of Psychology and Education, had suggested in his published work and in his private investigations those opportunities for systematic experiment which were so slowly taken up.

[76]Bartlett, F.C. (1955) op. cit., p.207.
[77]Kenna, J.C. (1969) Chairs of psychology in British universities. *Supplement to the Bulletin of the British Psychological Society*, 22: 9-13.

CHAPTER 3

THE INTRODUCTION OF ANIMALS INTO THE LABORATORY: THE SCIENTISTS AND THEIR METHODS

The coverage of animal psychology in the *British Journal of Psychology* between 1904 and 1940 was comparatively limited. Greater emphasis was placed on educational, human performance and statistical questions. Much of the treatment of problems in animal psychology took essay form and was not centred on the experiments of the author but on those of foreign, normally American, workers.

C.S.Myers was certainly convinced of the need for the use of animals in psychological research. F.C.Bartlett records that his wife (E.M.Smith) attended Myers's 1909-11 lectures at Cambridge, where a predominant topic was 'current researches into the behaviour of simple organisms of insects and of more developed mammals; this undoubtedly because Myers was himself intensely interested. The earlier conditioning work of Pavlov was considered in detail.'[1] In his autobiography, Myers recounts: 'I was also responsible for getting an examination in psychology included at Cambridge in the choice of so-called special examinations in the curriculum for the Ordinary (pass) Degree for B.A. In this examination established in 1911, animal and educational psychology could be offered as additional optional subjects' and it was Smith who undertook to run the related course in Animal Psychology.[2] Myers also persuaded Cambridge to establish a Diploma in Psychological Medicine, with compulsory papers and practicals in both neurology and psychology.[3]

A significant early contribution to practical experiments with animals in Britain was made by women psychologists. As an emerging subject psychology represented a clear opportunity for women to begin to participate in the academic community within a new field that had not become characterized by male exclusivity.[4] Their terminology

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[1]Bartlett, F.C. (1965) Remembering Dr Myers. *Bulletin of the British Psychological Society*, 18, 58: 1-10.
[2]Myers, C.S. (1936) Charles Samuel Myers. In: Murchison, C.A. (ed.) (1936) *A history* of psychology in autobiography. Vol. III. Worcester, Mass.: Clark University Press and (1961) New York: Russell & Russell. It is important to note at this point that students choosing psychology would be examined in six topics, but that the sixth required *either* 'Application to Education' *or* 'Animal Psychology'. No clearer indication can be given of the different perceptions of the theoretical and applicable links between these two subject areas which existed at the time in Great Britain and the USA.
[3]Rodger, A. (1971) C.S.Myers in retrospect. *Bulletin of the British Psychological Society*, 24: 177-84.
[4]Solly Zuckerman's future father-in-law expressed reservations about Zuckerman's wish to marry his

was never behaviourist, although the experiments themselves usually reflected the current interests in Pavlovian conditioning or of those establishing learning theories and then behaviourism across the Atlantic; and a wide range of species was investigated, notes often being made on questions of suitability and technique. It is clear that Smith, encouraged by Myers, helped through her experimental work to make known in Cambridge the nature and potential of conditioning and behaviourism, but that in the light of the knowledge afforded by her work, opportunities to develop it fully were not taken. Lack of interest could not therefore be attributed to lack of knowledge, and Smith's marriage to Bartlett did not result in any greater enthusiasm for animal psychology on his part.

E.M.Smith

The 1912 edition of the *British Journal of Psychology* described 'Some observations concerning colour vision in dogs' by Miss E.M.Smith (from the Cambridge Psychological Laboratory, working as the Marion Kennedy student assisted by Newnham College).[5] This was the first generally available account of any animal experiment based in a British psychological laboratory. Smith adopted a scientific rather than anecdotal approach. She was supervised by Myers, who suggested the subject and methods. Reference was made to the breeds used, and to the weaknesses of previous experimental methods. A description was also given of the apparatus for the experiment, its dimensions, method of operation with trap-doors, and its facility to supply electric shocks as punishment. The experiments took place each day between 9.30 a.m. and 1.00 p.m. intermittently, but for a series of set periods between December 1909 and December 1910. Three of the seven dogs proved unsuitable during the preliminary familiarization and training with the equipment. One more later proved unsuitable, and only one completed the whole test. The merits of stimulation by reward and punishment (as advocated by Yerkes) were discussed, and it was found that even the use of slight shocks was unsuccessful because they produced either apathy or intense fear. Such fear prevented the dog approaching the shutters for several days and it was not possible to find a suitable level of electric current. All levels were low, but Myers suggested the strengths were heightened by perspiration of the pads of the paws. One dog cowered and trembled for two months after the first

daughter because women were still regarded as second class citizens in the academic environment of Oxford by 1939. (Zuckerman, S., 1978, *From apes to warlords: an autobiography 1904-46*. London: Hamish Hamilton, p.104.)

[5] Smith, E.M. (1912) Some observations concerning colour vision in dogs. *British Journal of Psychology*, V, 2: 119ff.

punitive stimulus, and the best experimental animal remained affected by the experience of shock for the duration of the series of experiments. The dogs were given two meals a day, the first after 1 p.m. if the experiments took place in the morning, or at 7 a.m. (followed by exercise) if they took place in the afternoon. The dogs were kept 'free and in and out of the house'. Smith explained that the chief disadvantage of the method was the inadequacy of the system of reward or punishment. The dogs could become bored or tired, or they could give up trying if the experiment became too difficult. Electric shock was soon abandoned as an unsuitable motivation. Smith writes in a rather sentimental and anthropomorphic manner, and remarks on the value of the holidays the dogs were given for the maintenance of interest in the experiment. She also describes the necessary considerations for the design of animal experiments. Tables are given describing the number of experiments and their dates.

The *Transactions* of Sub-section I of the British Association for the Advancement of Science in 1913 include 'A Preliminary Note on Habit Formation in Guinea Pigs' also by Miss E.M.Smith (later Lady Bartlett):[6] she reported that the observations on which her paper was based were carried out under the direction of C.S.Myers at the Cambridge Psychological Laboratory earlier that year. They formed part of a larger scheme designed to test the inheritability in guinea-pigs of such characters as rapidity of learning, ability to profit by practice, accuracy of performance, retentiveness, etc. With this end in view, and in the hope of discovering well-marked differences of behaviour, the animals were subjected to certain tests. The tests used were: a) the Labyrinth Test, and b) a new form of Sensory Discrimination Test, in which photic and auditory stimuli were combined. Smith said that despite the fact that this preliminary investigation was, owing to its scope, necessarily somewhat general in character, it had nevertheless brought to light several hitherto unrecorded points of interest concerning guinea-pig behaviour. The subject was again dealt with by Smith in proceedings of the British Psychological Society in 1920 under the title 'Habit Formations in Guinea-Pigs'.[7]

The investigation of mind in animals[8] was described as a brief but excellent survey, dealing with a variety of animal species from the protozoa to mammals, in which Smith showed a remarkably sound judgement in her selection of topics for discussion. She was 'among the first in this country to appreciate Pavlov's work, and in her account of

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[6]Smith, E.M. (1913) A preliminary note on habit formation in guinea pigs. *British Association for the Advancement of Science: Reports*, Sub-sectional Transactions - I, p.680.
[7]Smith, E.M. (1920) Habit formation in guinea pigs. *British Journal of Psychology*, XI: 177.
[8]Smith, E.M. (1915) *The investigation of mind in animals*. Cambridge: University Press.

instinct clearly anticipated the ethologists of the next generation. Her account of homing noted the role of experience and the use of visual landmarks, emphasized the complexity of the phenomenon, and discussed as improbable the telepathic hypothesis which had already been broached.'[9] It was Smith's intention, as described in her preface, to present 'a brief account of the modes of procedure employed by Animal Psychology, its aims, trend, and the general nature of the results hitherto obtained', using description and illustration.[10] Those acknowledged for their advice included C.S.Myers, C.L.Burt, and, on the subject of hormones and instinct, J.T.Cunningham. Her book contains reviews of the more important foreign work by such as Yerkes and Thorndike, but she referred to some simple experiments which are unattributed and with which she herself may have been involved. These include, for example, studies of learning and habit formation in the small fish Gobius, and conditioned response in the tube-worm Hydroides dianthus. Passing reference only is also made to experiments undertaken by Triplett, Parker and others, which may have been conducted in Britain but for which no further details beyond these surnames are given.

Beatrice Edgell

Beatrice Edgell of Bedford College for Women established one of the first experimental laboratories for psychology in Britain, and although she founded no school of psychology, the success of her work was shown by that of her students in many different fields.[11] For herself, Edgell[12] had been inspired by Lloyd Morgan when he had come to lecture at a college society in Aberystwyth in 1891 or 1892: she had been persuaded to hear him by her room-mate, who had worked under him at Bristol.

In the proceedings of the British Psychological Society on 8 November 1913,[13] 'Observations on the process of learning and relearning in mice and rats' were described by Mary E. Macgregor, introduced by Beatrice Edgell. This work was published in 1915 by the University of London Press as part of *Psychological studies from the Psychological Laboratory, Bedford College for Women, University of London*. The volume contains four separate experimental studies, introduced by

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[9]Hearnshaw, L.S. (1964) *A short history of British psychology 1840-1940*. London: Methuen, p.232.
[10]Smith, E.M. (1915) op. cit.
[11]Smith, M. et al., (1949) Obituary notice: Beatrice Edgell, 1871-1948. *British Journal of Psychology*, XXXIX, 3: 121-2.
[12]Edgell, B. (1931) Letter to C.Lloyd Morgan, 22 March. Bristol University History Collection: DM 128/486.
[13]*British Journal of Psychology*, vol.VI: 455.

Beatrice Edgell. Only the first ('A study of learning and relearning in mice and rats. Observers: M.Macgregor and J.Schinz') is based on animal work. The studies were made:

> ... as part of the regular work of the class held in connection with an Inter-Collegiate course of lectures on Memory, Association, and Thought Processes, Sessions 1912-13 and 1913-14 ... The problems dealt with are those raised by the lecture work of the two sessions, and the papers, for the most part, represent the repetition of experiments on the lines of previous investigations rather than the attack of new problems by new methods. The studies, therefore, do not claim to be 'original' research. This seemed to be a reason for publishing them in their present form instead of seeking to publish any portion of them in a psychological or philosophical journal.

Macgregor and Schinz used Yerkes's 'Straight' and 'Square' mazes as well as their own five-section type built for their experiments. They were kept clean with carbolic and 'Thymol', and this was not thought to affect the error curve. The relearning tasks were based on a requirement to run the mazes successfully in reverse. The rats were presented with Small's 'Spring Door', 'Spring Door Complicated' and 'Sawdust' puzzle-boxes. Very limited numbers of animals were used, one being discarded only after a whole term because of the discovery of its blindness, and it appears that because of 'wild and scared' behaviour in earlier stages, no 'gentling' or use of a domesticated laboratory strain was employed. Furthermore, reference is made to 'fresh' and 'new' experimenters and their added effect on the level of ability of the animals to produce realistic results. It seems that during the time the series of tests were carried out, Macgregor and Schinz were not always able to give the work their personal attention; or at least they shared it with other members of the class to which Beatrice Edgell refers.[14]

Victoria Hazlitt

A student of Bedford College, Victoria Hazlitt graduated in philosophy, with experimental psychology as a special subject, in 1910. After a position as assistant to the Professor of Education and Professor of Psychology at Colorado State University between 1912 and 1914, she was appointed part-time assistant and then demonstrator

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[14]Edgell, B. (1915) Introductory note. In: Edgell, B. et al. (1915) *Psychological studies from the psychological laboratory, Bedford College for Women, University of London*. London: Hodder and Stoughton, p.vii; Macgregor, M. and Schinz, J. (1915) A study of learning and relearning in mice and rats. In: Edgell, B. et al. (1915) ibid., pp.1-10.

and assistant lecturer in psychology at Bedford College until 1919. The war helped her career, as she was asked to act as temporary part-time lecturer in experimental psychology at King's College London and to maintain the associated laboratory while the regular member of staff, Dr Brown, was on war service. She also became the University's Curator of Psychology Apparatus in 1918, full-time assistant lecturer in experimental psychology in 1919, and lecturer in 1921, with a life appointment confirmed from 1926.[15] For many years she served as a Council member of the British Psychological Society.

Victoria Hazlitt was throughout these years the College's specialist in animal, experimental and child psychology, and archival evidence suggests that she undertook her work with quiet ambition and intensity. By 1924 she had abandoned her practical animal work, probably for lack of institutional facilities as referred to by Beatrice Edgell, and concentrated more on theory and child psychology, taking twelve months' leave of absence that year to complete the research that resulted in her book *Ability* published by Methuen in 1926, and for which the University awarded her a D.Litt. At the meeting of the Psychology Life Appointment Committee that same year she 'wished the Committee to realize that much publication work could only be accomplished at the expense of her teaching and that she did not anticipate bringing out another book for some little time to come'. Handwritten notes on the papers of this committee, probably Hazlitt's or Edgell's, also throw light on the working constraints of the time: '... conditions of a lecturer make it impossible to do much more ... much publication makes it impossible to do adequate teaching work ... keeping abreast of a subject like psychology means a great deal of time ... publishers want all the book ...'.[16]

Again in 1926, Hazlitt applied for a Readership in child and animal psychology. The Council gave its support but the Senate refused. Another application was made by her in 1931, but Council decided to delay its approval for submission, first until the autumn of that year and then until April 1932, on the grounds that the application should be as strong as possible in order to avoid a second refusal from the Senate. The decision of Council in April 1932 is not known, but that month Victoria Hazlitt died while cleaning a dress with petrol in a passage at the side of her house. She was killed by asphyxia, following burns, due to the ignition of her clothing. The coroner was unable to solve the mystery of the fire: 'I am going to be careful in my verdict because

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[15]Report of the Psychology Life Appointment Committee, 25th March 1926. RHUL Archives, AR 150 / D239.76.4. Her life appointment was later confirmed, and took effect from 1st September.
[16]Personal file of Victoria Henrietta Hazlitt. RHUL Archives, AR 150 / D239.

I have not sufficient proof of how it happened.'[17] *The Daily Mail*[18] claimed that 'it was suggested she lost her life because her scientific training prompted her to refrain from calling for help: "She might have thought, when the flames leaped about her", a psychologist said to a *Daily Mail* reporter, "that she would conserve her energy for putting out the fire rather than scream for help. A strong-willed and highly trained psychologist might think that"'.

Details in the *British Journal of Psychology* are given of studies in 'The acquisition of motor habits' by Victoria Hazlitt undertaken between 1917 and 1919 at the Psychology Laboratory, Bedford College, where she was completing postgraduate research under the supervision of Dr Beatrice Edgell. The purpose of her experiments was to ascertain whether practised rats learn a new maze more quickly than unpractised ones; and whether there are any characteristic differences between the behaviour of practised and unpractised rats in a new maze. Reference was made to E.M.Smith and her interpretations in *The investigation of mind in animals* (1915): unlike Hazlitt, she thought a modification to a habit would make a further one more difficult. The present experiments were designed to test this hypothesis and the factors involved. A full description of method is given. Mazes were seen as suitable because they provided a natural activity for a rat, and because they could have endless variety without involving any novel activity, 'whereas it is difficult to make a series of puzzle-boxes of even approximately equal difficulty'. The mazes were of wood, with 6-inch walls and alleys 4.5 inches wide. The runs were scrubbed with a very strong solution of Jeyes' fluid at frequent intervals, and grease-proof paper coverings further helped to guard against the rats' use of the scent of their own or another's tracks leading to food in the goal. The rats at first had to run the maze only once, and were used only if 'lively, healthy and nimble'. Twenty-two rats took part: most of them were confident and eager to enter the maze, but some behaved abnormally, and it is clear that, as with E.M.Smith's experiment with dogs, techniques for laboratory animal selection and acclimatization were not yet properly developed. Rat 'M' feared the operator and maze and at first tried to escape; then it became lethargic and was soon found dead in its bed-box. Rat 'J' was withdrawn and unco-operative, and at first 'I' would enter the maze and promptly fall asleep. Instances of fear produced attempts to escape, starting, jumping at the walls, or 'position habits' accompanied by 'glazed' eyes, and a cover was later added to the maze.

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[17] *News of the World*, 24 April 1932.
[18] 21 April 1932.

Like Smith's, Hazlitt's attitude to the animals was a little sentimental and anthropomorphic, and she refers to one 'not being upset by making a mistake'. She was clearly not possessed of the lean experimental objectivity that was currently accompanying the rise of behaviourism across the Atlantic, and believed that rats behaved ideationally rather than mechanically. However, her interest in the laboratory study of animal learning, which was expressed in her new and pioneering work on return to Great Britain, had no doubt been stimulated by discussions of the work of Thorndike and other American scientists during her time at Colorado State University, when she had the opportunity to consider the potential of animal experimentation in learning theory, according to the American methodologies then developing. 'The acquisition of motor habits' was her first published work, and she gave in it an

> ... indication of her general psychological outlook by a vigorous rejection of any quasi-mechanistic theory of learning ... [she ascribed] the transfer of skill shown by rats to a factor which, however lowly and indeterminate it might be, must be termed ideational. The readiness of the trained rats to deal with the problem presented by a new maze showed, she held, an appreciation of the general situation which must depend upon a consciousness of meaning, and this, since it goes beyond immediate sensation, can and should be called ideation. To interpret their behaviour thus did not mean that it was necessary to ascribe explicit conscious process to the animals, for even in man ideation is not to be identified with conscious processes.[19]

In 1920 she addressed the British Association for the Advancement of Science on 'Conditions of learning compared in man and rats,'[20] her paper appearing in *Nature* and other journals, and an article on 'Learning in man and animals' was published in *Discovery* in January 1921.[21] At a later date she turned to account her experience of

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[19]Wolters, A.W. (1933) Obituary: Victoria Hazlitt, 1887-1932. *British Journal of Psychology*, XXIII, 3: 205-8.

[20]Hazlitt, V. (1920) Conditions of learning compared in man and rats. *British Association for the Advancement of Science: Reports*, Sub-sectional Transactions - I, p.371.

[21]In this article she hinted at the areas of overlap between the work of the traditional circus trainer and the scientific psychologist in establishing methods for training and learning, and proposed evidence of similarities between human and animal learning processes. Her discussion was especially interesting in the light of the recent use of circus trainers to attempt to train sealions to detect enemy submarines in the First World War. 'When animal learning is mentioned, the mind is apt to conjure up pictures of a dog sitting with a piece of biscuit on his nose, or of an elephant dancing, or of some other unusual and unnatural feat. It is perhaps for this reason that we are inclined to think of the animals' learning process as quite different from our own. In view of this tendency it may prove interesting to institute a comparison between the laws of learning in man and in an animal as low in the scale as a rat ... It has been found that the number of repetitions for learning a long series is disproportionately great when compared with the number for learning a short series ... Another fact which has been established experimentally is that the number of repetitions necessary for learning a given series by heart is affected by the distribution of the repetitions ... A third group of facts which

the pitfalls encountered in the study of animal behaviour: her experience with animals in the laboratory had led her to feel able to criticize in an article Mc Dougall's experimental work on Lamarckian inheritance for its procedural shortcomings. Later, F.A.E.Crew carried out a repetition and re-examination of Mc Dougall's Lamarckian experiment and reported on it in the sectional transactions of the British Association for the Advancement of Science in 1936: he used eighteen generations of about 2,500 rats, and, like Hazlitt, did not believe that Mc Dougall's findings were valid.[22]

In her obituary notice, Wolters recorded that Hazlitt 'regarded the processes of animals' learning as being thoroughly continuous with those of human beings, and as revealing intelligence and insight comparable with those of man'. She therefore united the new interests in learning behaviour as being developed in the United States with the outlook of a truly comparative psychologist, by that time a rare breed on either side of the Atlantic. She rejected every kind of psychological atomism and insisted on the organic unity of the individual as the fundamental fact of mental life. *The Times* of 25 April 1932 reported that 'Dr Hazlitt was just reaching the fullness of her power both as an original thinker and as a teacher ... Behind her careful observation of facts lay a keen interest in the ultimate problems of psychology'.

G.C.Grindley

It is appropriate that Lloyd Morgan's contribution to animal psychology should be marked by the fact that some of the most significant animal work of this new phase of restricted experimentation in the early 20th century was carried out by a researcher who also worked at Bristol, G.C.Grindley. Grindley, trained as a physicist, had worked for some years as a research assistant in the Department of Physics at Bristol, where a senior colleague, A.P.Chattock, a retired Professor of Physics, gave him encouragement and collaborated with him in the study of learning in young chickens. (Chattock's own interest in animal behaviour had been stimulated when in retirement

has been established with regard to learning by heart concerns the most economical division of the material ... Another aspect of human [and animal] learning is that the acquirement of one habit usually makes it easier to acquire another similar to it ... Judging from the evidence at hand, there is an extraordinary resemblance between the laws of animal and human learning when the task concerned is the acquisition of motor habits. The inquiry into the subject of the differentiation of human from animal learning on levels higher than that of the acquisition of motor habit offers a fascinating field for research. While a great deal has been written on the subject, there has been comparatively little exact experimental work.'

[22]Hazlitt, V. (1927) Professor McDougall and the Lamarckian hypothesis. *British Journal of Psychology*, XVIII: 77-86; Wolters, A.W. (1933) op. cit.

after 1910 at his poultry farm he began, under the auspices of the Ministry of Agriculture, to attempt improvements in artificial incubation.) The Professor of Philosophy, G.C.Field, also gave considerable support and invited Grindley to lecture on psychology to his philosophy class, thereby helping to make Grindley's practice of psychology secure.[23]

In his 'Experiments on the "direction of associations" in young chickens' at the Department of Philosophy at Bristol, communicated for publication by Lloyd Morgan, Grindley studied the directions in which secondary neural connections may be formed. The methods were Pavlovian, ten-day-old chicks being conditioned with a horn stimulus. An attempt was made at 'negative learning' when rice was used that had been soaked in a solution of quassia extract. The experiment was spoilt because nearly all the chicks either stopped pecking at the rice or failed to notice a change in it. A 'sharp' electric shock was therefore substituted for the noxious rice, but with similar difficulties. Finally, conditioned response was examined by pairing the horn with a shock to the feet delivered via a metal mesh-floored cage. Grindley concludes that normal 'onwards' conditioned response became evident in the trials, but that the 'reverse' association group remained as unconditioned as the control group.[24] During the carrying out of these experiments Grindley received extensive advice and written notes from Lloyd Morgan,[25] who considered that two stories, though inseparable, should be distinguished from the work: 'a behaviouristic and physiological story in terms of stimulus and response under the concept of physical influence' and 'a mental story in terms of reference, enjoyment, and guidance of procedure ... Let us grant that the chick is body-mind, however body and mind may be related'. He noted the difficulty of identifying any primary responses to stimulation in the chick: there was no equivalent of the pricking of a dog's ears to observe. It was Lloyd Morgan who suggested the soaking of the rice in quassia or quinine and later the use of slight electric shocks to produce negative stimuli to compare with the effects of the tapping and horn stimuli already used in earlier experiments.

Grindley's 'The neural basis of purposive activity', published the following year, suggested that observation of normal and abnormal behaviour can contribute to an understanding of cerebral physiology: more observation of the effects of lesions was

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[23]Zangwill, O.L. (1977) Obituary: G.C.Grindley (1903-1976). *Quarterly Journal of Experimental Psychology*, 29: 1-3.
[24]Grindley, G.C. (1926) Experiments on the 'direction of associations' in young chickens. *British Journal of Psychology*, XVII: 210-21.
[25]Lloyd Morgan, C. (?1926) Notes on Mr G.C.Grindley's experiments... Bristol University History Collection: DM 612.

necessary. Grindley produced an essay illuminated with experimental evidence[26] and suggested further work on the 'E-cell' theory as supported by William McDougall.[27]

Soon afterwards, an article appeared in the *British Journal of Psychology* by C.V.D.Hadley of the Cambridge Psychological Laboratory on 'Transfer experiments with guinea-pigs'. 'Transfer experiments are attempts to specify and limit the kinds of changes which can be made in some situations without destroying the habitual reaction which the animal has acquired with regard to that situation.' Guinea-pigs were used with a reward rather than punishment stimulus. Moderate hunger was generated daily as an incentive: no food was given from 10 a.m. until the 5.30 p.m. trials. The behaviour of the animals during learning was seen to fall into phases : 1) the emotional phase of a) curiosity or exploration, b) fear with timidity, c) pugnacity, d) food-seeking and e) play or 'excitment'; 2) the phase of directed effort; and 3) the phase of perfecting the correct response. Some animals had to be discarded because of timidity and 'position habits', and Hadley was not sure of the age of the animals, a disadvantage of the 'play' phase. The transfer criteria were illumination levels and area-size, and Hadley believed that transfers were usually achieved as animals began to react to a new stimulus, as required.[28]

Sir Charles Sherrington wrote to Lloyd Morgan from the physiological laboratory, Oxford, in 1927, obviously interested in Grindley and his work:

> The other day at Manchester I mentioned to Pear the serious present day lack among our younger men of any interest in or working at what used to be termed 'psychophysics', i.e. sense organs (embracing physical - or chemical - stimulation, physiological reaction, and psychical reaction). He now writes me he had opportunity to speak with you, and that you think well of someone interested in such work at the University of Bristol. I ought to say at once that I have no appointment to offer in the subject - I wish we had such an appointment here - but I should be grateful nonetheless if you could give me information about anyone who is qualified for, and interested in, that kind of work, especially in auditory or visual. I could then, should opportunity offer, know where to look.[29]

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[26]It included that obtained by C. Lloyd Morgan concerning the learned pecking behaviour of chicks, and described in (1925) *Life, mind, and spirit*, Lecture IV. New York: Henry Holt & Co.
[27]Grindley, G.C. (1927a) The neural basis of purposive activity. *British Journal of Psychology*, XVIII: 168-88.
[28]Hadley, C.V.D. (1927) Transfer experiments with guinea-pigs. *British Journal of Psychology*, XVIII: 189-224.
[29]Sherrington, C.S. (1927) Letter to C.Lloyd Morgan, 29 March. Bristol University History Collection: DM 128/394.

Lloyd Morgan forwarded Sherrington's letter to Grindley, who replied to Lloyd Morgan with enthusiasm for an opportunity that did not eventually materialize: 'Thank you very much for sending on Sir Charles Sherrington's letter. It is extremely interesting to find that he wants people to do physiological psychology. Should he ever have a vacant post for which I might be "in the running", I should of course very much like to hear of it. I will send him a copy of the chick paper, as you suggest.'[30] By 1928, Grindley had taken up an appointment as acting demonstrator at the Cambridge Psychological Laboratory, but he maintained practical working links with Bristol, where he continued to experiment. He reported to Lloyd Morgan on his new circumstances at Cambridge: 'I like the Cambridge laboratory very much, and I think that Mr Bartlett is an extremely good chief.'[31]

In a critical notice by Grindley, soon after his arrival at the Cambridge Psychological Laboratory, of a translation of *Conditioned reflexes: an investigation of the physiological activity of the cerebral cortex* by I.P.Pavlov, he claimed that Pavlov's work could have revealed much more about the behaviour of dogs if more comprehensive recordings of their responses had been made, since the intelligence of dogs, their general behaviour and 'attitude' deserved more than mere recording of salivation. The eyes, ears and tail could show much more. Grindley 'would especially like to see the results extended very much further than has yet been done by any workers in this field to other animals than the dog and to other reflexes than the salivary reflexes.'[32] Lloyd Morgan wrote to Grindley over this review of Pavlov, and Grindley was able to supply answers to questions about Pavlov's findings by consulting Dr Anrep who worked with Pavlov for many years and who was still in close touch with him.[33] Although Pavlov had lectured on conditioned reflexes at Charing Cross Medical School in 1906, it was not until the translation of 1927 and that of his *Lectures on conditioned reflexes* of 1928 that his work became generally accessible in the United Kingdom, exactly at the time when the question of the state's relationship with science was beginning to be discussed against a background of social

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[30]Grindley, G.C. (1927b) Letter to C.Lloyd Morgan, 4 April. Bristol University History Collection: DM 128/395.
[31]Grindley, G.C. (1929a) Letter to C.Lloyd Morgan, 5 June. Bristol University History Collection: DM 128/429.
[32]Grindley, G.C. (1929b) Critical notice. *British Journal of Psychology*, XIX: 452-5.
[33]Grindley wrote to Lloyd Morgan: 'I have asked Dr Anrep ... about those experiments. He says that Pavlov found that there was something wrong with the results which he published, and he has withdrawn them. Pavlov has since tried to repeat the experiments under carefully controlled conditions, and he has found no satisfactory evidence of the inheritance of acquired habits or conditioned reflexes. Of course it is possible that Pavlov has not yet worked over a sufficient number of generations; but at any rate it seems clear that the early results were mistaken.' (G.C.Grindley, 1929a, op. cit.)

and economic upheaval. Pavlov was a good example of a scientist working within a totalitarian society which had, at least for ideological reasons, embraced and encouraged his theories and his work as a source for controlled national and social development.

At this time Grindley himself continued a comprehensive series of experiments to examine the learning process in chickens, frequently refering to American methods of studies, such as those of Yerkes and Dodson, which stimulated his own. In his 'Experiments on the influence of the amount of reward on learning in young chickens', seventy chicks were subjected to moderate hunger. To counteract loneliness in the experiment, 'companion' non-experimental chicks were tethered with string to the side of the area where the individual experimental chick was performing. The 'companion' chicks became reasonably quiescent after a few days of training. The result of the experiments was that as the rewards increased, so did the rate of learning, but because there were many individual differences amongst the chicks, accurate interpretations were not possible.[34]

With A.P.Chattock, who had also advised him during his earlier experiments, he then examined 'The effects of change of reward on learning in chickens'. A simple maze was used, with two types of food reward, the experiment being similar to that of M.H.Elliot of the University of California. Decoy chickens were again used to prevent 'loneliness'. It was found that a change of reward caused confusion, and some chicks disliked the food offered at either stage. Generally it was thought that the change had no effect on learning.[35] Chattock and Grindley[36] now turned to 'The effect of delayed reward on the maze performance of chickens'. They noted the uncertainty caused by the differing conclusions of previous American investigations using rats. In their own experiment there were again wide differences between individuals (a recurring problem with Grindley's chicks), but delays were seen to prejudice learning, as did the amount of reward given if reduced.

G.C.Drew and F.H.George[37] refer to Grindley's work when dealing with the role of reinforcement. It had been shown that stimuli which have been associated with food

[34]Grindley, G.C. (1929c) Experiments on the influence of the amount of reward on learning in young chickens. *British Journal of Psychology*, XX, 2: 173-80.
[35]Chattock, A.P. and Grindley, G.C. (1931) The effect of change of reward on learning in chickens. *British Journal of Psychology*, XXII, 1: 62-6.
[36]Chattock, A.P. and Grindley, G.C. (1933) The effect of delayed reward on the maze performance of chickens. *British Journal of Psychology*, XXIII, 4: 382-8.
[37]Drew, G.C. and George, F.H. (1953) Studies of animal learning. In: Mace, C.A. and Vernon, P.E. (eds) (1953) *Current trends in British psychology*. London: Methuen, pp.172-84.

can themselves acquire a 'goal significance', and the larger the reward, the faster the learning. Grindley also noted that the sight of food, even in the absence of actual ingestion, was reinforcing, since it led to a small, though transient, increment in the speed of locomotion. This was an early demonstration of the secondary reinforcing power of the mere sight of food, an important point for subsequent acquired-drive theories. Pavlov[38] had already proved that conditioned stimuli could serve as reinforcers in higher-order conditioning paradigms, but Grindley seems to have been the first to report the phenomenon in an instrumental-learning situation.[39] Grindley placed young chicks in a straight runway at the other end of which were grains of rice under glass, so that the chicks could see but not eat them. He found that running speed increased during the first four or five trials, indicating that learning was taking place, but that speed subsequently fell off. Secondary reinforcements ceased to be effective unless themselves reinforced by the primary ones from time to time. The amount of primary reinforcement was also important, as Grindley discovered. If the degree of hunger was held constant, the amount of learning depended on the value of the reward. Chickens were presented with relatively simple tasks, and when these were accomplished, they were rewarded with varying quantities of the same food. It was found that with hunger held constant, the speed of learning tended to depend upon the amount of food given as a reward. The greater the amount of food offered, the more rapidly the learning took place.[40]

Elsewhere, Grindley[41] referred to trial-and-error learning, stating that most experiments on it had dealt with the formation of rather complex habits. He had devised a simple experiment using guinea-pigs in which the action to be learnt was only a turn of the head to the right, in response to the sound of a buzzer. The animal stood on a wooden platform in a sound-proof room and its body was held still by means of a jacket. Head movements were rewarded with carrots, and a learning scale to record these 'superstitious' movements was devised. The surrounding conditions were made as uniform as possible. It was also found possible to train the animal to move its head in the opposite direction. Learning curves showed marked general improvement incorporating continual minor regressions on the way. These experiments were the subject of further correspondence between Lloyd Morgan and

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[38]Pavlov, I.P. (1927) *Conditioned reflexes: an investigation of the physiological activity of the cerebral cortex* (Translated and edited by G.V.Anrep). London: Oxford University Press.
[39]Brown, J.S. (1979) Motivation. In: Hearst, E. (ed.) (1979) *The first century of experimental psychology*. Hillsdale, New Jersey: Lawrence Erlbaum Associates, p.247.
[40]Katz, D. (1953) *Animals and men: studies in comparative psychology*. 2nd ed. London: Longmans, p.157.
[41]Grindley, G.C. (1937) *The intelligence of animals*. London: Methuen.

Grindley in 1932, and it is clear that, as with the chick experiments, a major topic for discussion remained the distinction between the 'mind story' and the 'body story'. Grindley wrote: 'I think that my guinea pigs probably "expected" food when they turned their heads; but I am not really concerned with the mind story. What I wanted to show was that the principle of "conditioning" is not sufficient, by itself, to explain the observed behaviour. "Conditioning", of course, is body story; but I don't feel that because "conditioning" won't explain the results one must therefore fly off into mind story.'[42]

Zangwill[43] remarked later that there was 'nothing of the ethologist' about Grindley, his experimental approach being extremely rigorous and being himself highly skilled in devising simple, yet effective, methods of studying the acquisition of simple behaviour patterns, as in the guinea-pig work.[44] The study of simple habit formation in guinea-pigs led him seriously to question the adequacy of Pavlov's position to explain the formation even of a very simple adaptive habit. As a result he supplemented it with a concept of reinforcement which owed much to Thorndike. Zangwill considered that 'Grindley's paper anticipated much subsequent work on what came to be called instrumental or operant conditioning' and B.F.Skinner was among those who paid tribute to its importance.

G.C.Drew

In describing the use of animals in experimental psychology, G.C.Drew and F.H.George later stated that it had the advantage of reducing the number of extraneous and uncontrollable variables.[45] But one effect of regarding them as an experimental convenience had been to restrict attention to a very few species which have proved suitable for learning experiments. They would like a broadening of the

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[42]Grindley, G.C. (1932) Letter to C.Lloyd Morgan, 10 November. Bristol University History Collection: DM 612.
[43]Zangwill, O.L. (1977) Obituary: G.C.Grindley (1903-1976). *Quarterly Journal of Experimental Psychology*, 29: 1-3.
[44]However, Grindley was on other occasions prepared to soften his outlook, as in 'The sense of pain in animals' (1933, *Animal Year Book*, vol. 2, University of London Animal Welfare Society. Revised version published as a pamphlet with the same title in 1959 by the Universities Federation for Animal Welfare, London). Here he commented: 'It is true that the notion that the animal mind is altogether different from the human mind is dying out as the theory of evolution becomes more and more widely accepted ... If an animal behaves in the kind of way in which we behave when we have a certain thought or feeling, and if this happens in the kind of situation which produces this mental process in us, we may reasonably suppose that the animal has a similar thought or feeling.'
[45]Drew, G.C. and George, F.H. (1953) op. cit., p.173.

area of study to other species, and hoped that British psychologists would 'play a rather bigger part in the future than they have done in the past in the field of animal behaviourism. Perhaps it would not be out of place here to plead for more psychologists with some zoological training to enable us to see a little further than the rat'.

Like Grindley, Drew was one of a very limited number of animal psychologists experimenting in Britain in the 1920s and 1930s. In 1935, F.C.Bartlett enabled him to investigate 'The effects of a mixed incentive on the behaviour of rats' at the Cambridge Psychological Laboratory, in order to assess the relationship between mixed reward and punishment and the performance of a simple task. This work was directly stimulated by earlier and contemporary experiments in the United States of America involving E.L.Thorndike and R.H.Waters on the 'law of effect', and C.J.Warden and E.C.Tolman on animal motivation and purposive behaviour. Drew also acknowledges the help of Grindley throughout the experiment. The rats were fed one hour in twenty-four, immediately after the experiment, in which apparatus of elaborate construction was used so that the experimenter was not visible to the subjects. Fittings were sound-dampened, and the punishment bell of 60 d.b. above the human threshold 'distressed the rats considerably', many of which were specially bred in the laboratory. The animals were first taught to run to a food box, receiving a food reward during the learning process. They were then subjected to a mixture of incentive stimuli, a bell being added to a food incentive during part of the time they were in the food box. The effects of the food and bell separately were ascertained on other groups of rats. The mixture of stimuli produced varying results in individual rats during the first few trials, but then produced a quicker performance.[46] This experiment and the matter of incentives was later discussed by Grindley,[47] Katz[48] and Oldfield.[49] Drew himself again examined the subject of incentives in co-operation with K.S.Lashley at Harvard in 1937.[50]

Drew also carried out studies of 'The speed of locomotion gradient and its relation to the goal gradient',[51] from which he concluded that the former gradient could not

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[46]Drew, G.C. (1935) The effects of a mixed incentive on the behaviour of rats. *British Journal of Psychology*, XXVI, 2: 120-34.
[47]Grindley, G.C. (1950) *The intelligence of animals*. 2nd ed. London: Methuen, p.55.
[48]Katz, D. (1953) op. cit., p.159.
[49]Oldfield, R.C. (1953) The place of experiment in psychology. In: Mace, C.A. and Vernon, P.E. *Current trends in British psychology*. London: Methuen, pp.138-51.
[50]Drew, G.C. (1938) The function of punishment and learning. *Journal of Genetic Psychology*, 52: 257-67.
[51]Drew, G.C. (1939) The speed of locomotion gradient and its relation to the goal gradient. *Journal*

easily be used to support the goal gradient hypothesis. In 1936, working with a Medical Research Council grant at the Cambridge Psychological Laboratory, Drew investigated 'The recurrence of eating in rats after apparent satiation'.[52] This thorough investigation, employing laboratory-bred and dealer-supplied rats in a series of 'place', 'retrieving', 'effort' and 'stimulus' experiments, again involved comparisons with and reference to foreign work such as that of Pavlov, Skinner, Hull, Lashley and Stone. Preliminary training of the experimental rats had in fact included experiments on a model of Lashley's Maze III. The investigation itself found that a recurrence could take place under conditions of excitement, and also that such excitement would correspondingly prevent eating in hungry rats. This appeared similar to Pavlovian 'external inhibition' and 'disinhibition', and it was concluded that satiation must involve some mechanism similar to Pavlov's 'internal inhibition'. In this work Drew was again advised by F.C.Bartlett and G.C.Grindley, whose pupil he had become, and also by Professor George Humphrey of Queen's University, Kingston, Canada, who later became Professor of Experimental Psychology at Oxford.

The Rockefeller Foundation supported Drew and the Cambridge Psychological Laboratory, and in his report to it on the period 1937-1942 Bartlett stressed the continued need for pure research as well as research for applied purposes, and announced that Drew had left to head the new department at Bristol after his spell as Director of Training Research in the RAF. In 1937 the University had agreed to use the Wilson Bequest for an expansion in experimental psychology, and the Rockefeller Trustees made a generous gift to the laboratory for equipment and research. These were the first two major endowments ever received by the department. 'Drew's original work on animals, followed, when the war broke out, by his experiments on "skill fatigue" have brought him one of the key positions of psychological development in the country.'[53] It is tempting to link Drew's animal work with theories of display and control as studied at Cambridge, which were Bartlett's area of interest and also relevant to the war effort.

Investigations at the Cambridge Psychological Laboratory at this time into internal inhibition were described by R.C.Oldfield[54] in 'Some recent experiments bearing on

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of Comparative Psychology, XXVII: 333-72. Cited by Drew, G.C. and George, F.H. (1953) op. cit., p.183.

[52]Drew, G.C. (1937). The recurrence of eating in rats after apparent satiation. *Zoological Society of London. Proceedings*, 107: 95-106.

[53]Cambridge Univ Lib. MS Room. Sir Frederic Bartlett, undated, c1945. Add. MS. 8076. D.1.4.

[54]Oldfield, R.C. (1937) Some recent experiments bearing on 'Internal Inhibition'. *British Journal of Psychology*, XXVIII, 1: 28-42.

"internal inhibition"'. The two conditions favourable to the production of internal inhibition as described by Pavlov were seen to be a) uniformity of sensory field and b) failure of the response to satisfy a drive. Oldfield referred here to the animal work, published and unpublished, of A.F.Rawdon Smith, R.J.Pumphrey and G.C.Drew. Pumphrey, a zoologist, and Rawdon Smith[55] studied the behaviour of the last abdominal ganglion in the cockroach under direct electrical stimulation, comparing the artificial impulse entering with the impulse leaving the ganglion and noting the excitory effect of irregular stimuli.

[55]Pumphrey, R.J. and Rawdon Smith, A.F. (1937) Behaviour of the last abdominal ganglion in the cockroach. *Royal Society of London. Proceedings. Series B. Biological Sciences.* CXXII: 106-18.

CHAPTER 4

INVESTIGATIONS BEYOND THE PSYCHOLOGIST'S LABORATORY

Introduction

From the turn of the century until the Second World War studies in comparative and animal psychology were subject to the effect of complex relationships with other disciplines involving the experimental investigation of behaviour. The rise of Behaviourism in the United States of America soon came to be criticized by many laboratory-orientated psychologists in the United Kingdom who felt that it could not fulfil the potential of scientific research in psychology. Such criticism (as from C.S.Myers and F.C.Bartlett) was matched by that of zoologists such as E.S.Russell. This reaction helped indirectly to nurture ethology and in many ways deflected attention from laboratory-based animal psychology, which became more identified with the behaviourism that was clearly largely unaccepted in this country. Meanwhile animal behaviour became a subject of interest also to those who worked outside the animal psychology laboratory.

An inspection of the business of the various sections and the contents of their transactions as recorded in *Reports* of the British Association for the Advancement of Science will reveal that the subject of animal behaviour was from the beginning of the 20th century of interest not only to psychologists, and a frequent scattering of topics appears under the names of those both within and without psychology, and sometimes beyond the psychologist's laboratory. For example, in 1912, G. Elliot Smith, the anatomist, described the evidence of primate cerebral anatomy as a source for a better understanding of human behaviour via comparative psychology. The difference in behaviour of a series of primates and the variations in their responses to electrical stimulation of their brains might be correlated with corresponding structural differences in these brains: the structural comparison of the human brain would then reveal extra information.[1] This was the subject of a presidential address to Section H (Anthropology) of the British Association for the Advancement of Science. The psychologist J.L.McIntyre spoke in 1913 to Section I (Physiology)[2] on 'The role of

[1]Elliot Smith, G. (1912) Presidential address. *British Association for the Advancement of Science: Reports*, Sectional Transactions - H, p.575ff.
[2]In his presidential address to the British Association (*Reports*, 1931, p.181), C.S.Myers recalled: 'Psychology was specifically recognized by this Association as a separate Science in the year 1913, when for the first time it was constituted a Sub-section under Physiology, which had itself been

memory in animal behaviour' and on the matter of comparative psychology and the evolution of behaviour, including the notion of 'free ideas' in animals.

T.H.Savory began to study spiders in 1913. By 1916, he was discovering the way a spider ordered the movement of its legs by first tiring some spiders on the surface of water and then observing them drag their weary legs over a dry surface.[3] He also kept spiders in a dark environment so that egg-laying during the day might be observed. Savory, an exhibitioner of St John's College, Cambridge, gave dramatic accounts of the male and female spiders, their webs and the flies he introduced to their cage.[4] His account in *Science Progress* was intended for popular consumption, but later accounts, showing his continued application to the subject, were more sombre, for example 'Evolution in spiders: an essay in phylogeny'[5] and 'Experiments on the tropisms of spiders.'[6] By 1936, he had published two books, one on *Mechanistic biology and animal behaviour.*[7] It was in essay form and dealt mainly with invertebrates. He advocated objective and deterministic rather than anthropomorphic study, saying that those who felt that mechanistic interpretation was inadequate might adopt the teleological or purposive view of animal behaviour. Although we might 'know' a domestic animal like a dog, he said, we cannot enter the inner psychical life of an invertebrate. He dealt with reflexes, tropisms, instinct, habit and evolution, and concentrated largely on his spiders. He carried out Pavlovian experiments on these, by using the vibrations of a tuning fork as conditioning stimuli, noting that changes in vibration frequency in a different instrument revive the interest of spiders whose response had in the earlier one been extinguished through the absence of any following unconditioned stimulus. This work is reminiscent of the contemporary experiments described by Oldfield.[8]

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established as an independent Section (distinct from Biology) in 1893'. In Bournemouth at the 1919 meeting, among the Resolutions and Recommendations referred to the Council for consideration and if desirable for action was a proposal from Section I that Council change its name from Physiology to Physiology and Psychology, and that presidents in alternate years represent the two branches of the Section. In 1920 Section I recommended a separate section for psychology, and this was approved by the General Committee, subject to approval by Council. In 1921 Council approved the formation of Section J (Psychology), and it met under the presidency of C.Lloyd Morgan.

[3]Savory, T.H. (1916) Some results of observations on the economy of the house spider, tegenaria atrica. *Science Progress*, 11: 246-50.

[4]Savory, T.H. (1917) Further notes on captive spiders. *Science Progress*, 12: 322-4.

[5](1926) *Science Progress*, 20: 475-80.

[6](1934) *Science Progress*, 28.

[7]Savory, T.H. (1936) *Mechanistic biology and animal behaviour*. London: Watts & Co.

[8]Oldfield, R.C., (1937) Some recent experiments bearing on 'Internal Inhibition'. *British Journal of Psychology*, XXVIII, 1: 28-42.

In 1922, C.S.Sherrington, as President of the British Association for the Advancement of Science, devoted himself to 'Some aspects of animal mechanism,' inevitably a subject of continuing interest to psychologists, as he himself realized. In 1929, G.E.Coghill published *Anatomy and the problem of behaviour*, in which 'genetically based' behaviour in salamanders was described. Another anatomist, S.Zuckerman, described his work at London Zoo in *The social life of monkeys and apes.*[9] The transactions of Section D (Zoology) of the British Association for the Advancement of Science in 1933 included an account by H.O.Bull of the experimental study of conditioned responses in fishes, and, in 1934, the transactions of a joint discussion between Section J (Psychology) and Section D on 'The interpretation of animal behaviour' included an 'Analysis of the maternal drives in the rat' by B.P.Wiesner, based on his work and that of N.M.Sheard in Edinburgh in 1933.[10]

As 1940 drew near, work by those other than psychologists acquired more prominence in the field of animal behaviour. Of course, laboratory work itself continued. E.G.MacGregor[11] reported on 'Odour as a basis for orientated movement in ants' from the Sub-department of Entomology, Department of Zoology, Cambridge. His research had begun in 1938 and involved the use of (some artificial) ants' nests as conditioning stimuli: he concluded that a superfluity of senses results in complicated movement in the ant. Precise, technical and exhaustive research was published by W.H.Thorpe after work in the same laboratory: 'Olfactory conditioning in a parasitic insect and its relation to the problem of host selection;'[12] 'Further experiments on olfactory conditioning in a parasitic insect. The nature of the conditioning process;'[13] and 'Further studies on pre-imaginal olfactory conditioning in insects.'[14]

Just as some scientists outside psychology made significant contributions to animal behaviour studies so, too, psychologists sometimes became involved in animal studies

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[9](1932) London: Kegan Paul and Co.
[10]Wiesner, B.P. and Sheard, N.M. (1933) *Maternal behaviour in the rat.* Edinburgh: Oliver and Boyd. Experiments had demonstrated that mother rats will retrieve (carry to the nest) a wide variety of young animals, but they may refuse rats smaller than but older than these: the decisive property of the 'object' seemed to be its age. An analysis was undertaken of physiological mechanisms inducing maternal behaviour: many virgin rats exhibited maternal behaviour after having been treated with anterior lobe extracts from the pituitary of mother rats (*British Association for the Advancement of Science: Reports*, Sectional Transactions-J, 1934, pp.380-1).
[11](1948) *Behaviour*, 1: 267-95.
[12]Thorpe, W.H. and Jones, F.G.W. (1937) *Proceedings of the Royal Society of London, Series B. Biological Sciences*, 124: 56-81.
[13]Thorpe, W.H. (1938) *Proceedings of the Royal Society of London, Series B. Biological Sciences*, 126: 370-97.
[14]Thorpe, W.H. (1939) *Proceedings of the Royal Society of London, Series B. Biological Sciences*, 127: 424-33.

that were not strictly psychological. The activities of K.J.W.Craik were an example of this. He became involved in a study of the 'Transient response of a primitive ear', that of a tortoise, and the work was purely physiological.[15] But 'many of the people he knew well and most deeply respected were trying to find mathematical expressions for a large variety of relations between stimuli and the responses which they set up in animals and human beings.'[16]

Early applied studies of animal behaviour: case-studies of military applications

The exigencies of the First World War resulted generally in a new appeal to and dependence upon science to provide solutions for the war effort, in terms both of industrial production and fighting efficiency. Although this reliance was somewhat resented when it began to intrude on the traditional areas of activity and responsibility of service personnel,[17] besides its significant practical worth it helped to establish various branches of science as worthy, publicly commendable, and sometimes indispensable. However, it would be wrong to claim that the scientific manipulation of animal behaviour to assist in the war effort achieved such acclaim and recognition. The use of 'sniffer dogs' and carrier pigeons was already established, quite well known to the public, and the result more of simple training than applied science. Furthermore, any attempt at an original and effective employment of animals in the war effort, based on scientific procedures and involving special research programmes supported by a government cautious about all forms of expenditure, as well as about the new threat of sophisticated espionage, would inevitably be cloaked in secrecy. The benefits accruing to the progress of the science itself, assuming successfully conducted research if not fully effective application 'in anger', would therefore be negligible.

A matter of very grave concern soon after the beginning of hostilities was the disastrous effect of the depradations of U-boats, whose large-scale and seemingly irresistible destruction of merchant shipping caused not only great loss of life but also a fear that the nation would be fatally starved of materials and food. Apart from this, the U-boat campaign represented an effective type of early psychological warfare which was based on the scientific and technological success of the enemy. It was in

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[15] Craik, K.J.W. et al., (1939) *Proceedings of the Physiological Society*, 18P-19P.
[16] Bartlett, F.C. (1946) Obituary notice: Kenneth J.W.Craik, 1914-1945. *British Journal of Psychology*, XXXVI, 3: 109-16.
[17] This resentment, and strained relations often resulting in inefficiency and poor communication, lasted well into the period of the Second World War, as described by S.Zuckerman (1978) *From apes to warlords: an autobiography 1904-46*. London: Hamish Hamilton.

these circumstances that the British government decided to attempt a response through a programme of secret research part of which depended itself on psychology and the effective control of behaviour - that of the sealion and seagull. The research would bring together the scientist and the circus-trainer, but the scientists represented marine biology and other disciplines than animal psychology, and there is no evidence that any of the few British animal psychologists who could have offered useful advice were appraised of this secret programme or approached for assistance.[18] After the end of the war, the manipulation of the behaviour of animals for military purposes was abandoned in this country but developed in the United States, where the principles of behaviourism were found to be most appropriate and applied to procedures such as the detection of submerged objects by dolphins and the guidance of missiles by pigeons which had been subjected to operant conditioning. In the British sea-lion experiments of the First World War, advice was also sought by the Admiralty from an American consultant, perhaps partly in recognition of the main contemporary source for expertise on behavioural manipulation and partly as a result of the interest this programme would therefore have held for the guest observer.

Sea-lions

Research connected with the experimental use of sealions to aid submarine detection extended from November 1916 to July 1917. At first an interest was shown in hearing in fishes, and in a memorandum of the meeting of the Sub-Committee of Section II[19] of the Admiralty's Board of Invention and Research held on 28 November 1916, the secretary, Sir Richard Paget F.R.S., reported an interview he had had with Dr E.J.Allen F.R.S., director of the Marine Biological Laboratory in Plymouth, who had undertaken to carry out experiments on this subject, and reference was made to some American work.[20] It seems that during the interview attention was shifted specifically to the potential of seals and sealions, which were intelligent and readily trained animals, and Paget's original thoughts were summarized in a note headed 'Suggested

[18]The help of other psychologists was enlisted after the formation by a group of businessmen of the Lancashire Anti-Submarine Committee in 1917, under the chairmanship of Professor Rutherford. Staff of the Cambridge Psychological Laboratory participated in the selection and training of personnel for hydrophone work. (Among the Cambridge staff was Miss E.M.Smith, the animal psychologist, but she was not invited to become involved in the work with sea-lions or birds described below.) Bartlett, F.C. (1937) Cambridge, England 1887-1937. *American Journal of Psychology*, 50: 97-110.

[19]This was one of six sections, and included in its area of responsibility the detection of submarines and mines.

[20]'Hearing in Fishes.' PRO ADM 293/5, p.271.

method of training of seals as submarine trackers' (11 December 1916) and reproduced in Allen's final report of the whole series of experiments delivered on 23 July 1917.[21]

Paget recommended the use of a muzzle to prevent the consumption of fish during training but which would not interfere through water disturbance with the animal's hearing powers. The aim would be to train muzzled animals prior to meals to ignore fish alongside them in a tank in favour of an artificial underwater sound, after a conditioned approach to which they would then be rewarded with food. Training would then be transferred to open water, using a submarine as the sound and food source, which the animals might learn to follow without the distraction of fish or sounds other than those associated with submarines. An animal on active service could be spotted each time it surfaced for air, and, having a suitably designed muzzle, 'if he could be taught to bark, namely, by way of inviting the submarine to come up and feed him, so much the better'. To recall the animal, a specially learned, additional under-water sound signal would be used: this would be necessary before the destruction of the enemy submarine, the sea-lion having learnt to jump on to a raft towed behind the moving parent ship.

The general purpose of these ideas was explained by Paget to the main Panel of the B.I.R. on 8 December 1916, and the current position summarized:

> It has been suggested that information on the question as to whether fish, seals and other marine animals can hear whilst swimming under water at speed may be useful as indicating the limits of speed possible for employing listening apparatus in moving vessels. Dr Allen ... has been in communication with ["]Captain["] Woodward [a showman], the trainer of seals and sea-lions, and experiments are now in preparation at Glasgow in one of the corporation swimming baths.[22]

Paget's suggestions formed the basis of the programme of experiments which were thenceforward supervised by Allen, who had started hearing studies of marine fishes at Plymouth but who soon turned to seals and sealions. Woodward had approached Professor Bragg of Section II earlier in 1916, presumably to introduce the idea of pressing sea-lions into the service of the nation, and in November Paget asked Allen to

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[21] Allen, E.J. (1917) *Report upon experiments on the hearing powers of sea-lions under water, and on the possibility of training these animals as submarine trackers*. B.I.R. 30051/17. London: Admiralty Board of Invention and Research. PRO ADM 293/5, pp.450-69.
[22] Minutes of the meeting of the Panel of the B.I.R., 8 December 1916. Report from Sir Richard Paget. PRO ADM 293/5.

travel to see the trainer, who was performing with two Californian sea-lions at Hengler's Circus in Glasgow. Demonstrations in the swimming baths followed, and Allen also raised with Woodward Paget's ideas on training for submarine tracking.

Woodward was left to develop the training programme and successfully conditioned three animals to respond appropriately to underwater sounds, as verified on 16 December by a Dr Albert A.Gray of Glasgow. Woodward also designed an effective muzzle[23] and was able to elicit disciplined directional response to artificial underwater sounds by muzzled animals in the company of live trout, and to conduct swimming speed tests at the Cranston Street baths. On 7 January 1917 he was joined by A.B.Wood of the Admiralty Experimental Station, Aberdour, at the open air swimming bath at Alexandra Park, Glasgow, to carry out more speed tests and to compare the hearing power of sea-lions with that of a watch type hydrophone, using a variety of sound-producing devices and noting the level of reliability of the experiments, and possible improvements, in view of factors which might have influenced the behaviour of the animals during tests.[24] The training and experiments continued until 10 February and were successful, and included a fourth animal, 'Queenie,' supplied on loan from the Zoological Society of London. Later in February Queenie and Woodward's 'Barker' performed successfully at the swimming baths at Great Smith Street, Westminster, in front of BIR Central Committee members Vice-Admiral Sir R.Peirse, Sir Charles Parsons and Sir Richard Paget, who made a detailed record of the observations,[25] as well as Allen. On this occasion improvements in the design of the experiments as suggested by Wood were incorporated. Work at Westminster continued for several weeks and more animals were trained, but it was clear that it was time for an open-water assessment of the sealion's suitability for its proposed duties in terms of disinclination to escape and controllability.

Lake Bala, up to four miles long and three-quarters of a mile wide, together with accommodation and small vessels, was made available by its owner, Sir Watkin

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[23]Muzzling was achieved by a wire cage attached by means of an elastic collar and a tape passing through the muzzle and across the animal's mouth. A small door in the front closed with a spring, and fish could be fed through it.

[24]Wood, A.B. (1917) *Behaviour of sea-lions towards subaqueous sounds*. B.I.R. 2228/17. London: Admiralty Board of Invention and Research. PRO ADM 218/20. A progress report was made by Paget at the meeting of the Sub Committee of Section II held on 9 January 1917 (PRO ADM 293/5 p.327) and it was noted that Allen was by then studying the structure of the animals' ears. It was added that seals were available in very large numbers and were said to be easier to train than any other animal.

[25]Paget, R.A.S. (23 February 1917) *Hearing of sea-lions*. In Allen, E.J. (1917) ibid., note 6, appendix III. Paget also later summarized the stage experimentation had reached by this time in a report to the Panel of the BIR on 9 December 1917 (PRO ADM 293/7).

Williams Wynn, Bart., and was the site of secret operations between 30 March and 6 July 1917. Stabling for about 50 sea-lions and a carpenter's shop were provided. Within a week, one sea-lion, 'Billiken,' would reliably respond to artificial underwater sound by approaching it over a distance of above 1,000 yards (nine minutes' swim). Various types of noise-making apparatus were used, including a 'large rattler' designed by Professor Bragg, audible under water at a distance of three miles, which could frighten the animals, and a mechanical 'pipe tapper' which was more consistent in sound level and reliability than the electric buzzers also used. Billiken managed controlled-response swims to the electric buzzer of one mile, 1,000 yards in 17.5 minutes at 5.4 mph, and one mile, 1,400 yards in 20.5 minutes at 5.3 mph, before a brief return to the music hall stage to replace Barker, who had died. But Queenie's performance was better, the best being three miles in 34.5 minutes at 5.2 mph, among a number of three-mile swims observed between 20 and 22 April by Sir Richard Paget and also by Surgeon Pleadwell of the United States Navy, who both made reports as a result.[26] Paget considered that a sea-lion with about two months' training was under as good control at a distance of two or three miles as a *well*-trained dog within range of a whistle, and that it was now time for open-sea trials.[27] Allen later noted, however, that the detection of specified sounds in a long, narrow lake would probably be less difficult than in the open sea, lacking the same reflective qualities and with a greater range of workable long-distance directions.

A problem to be resolved at Lake Bala was how to follow the animal's course when in active response mode over long distances. The sea-lion would remain submerged for up to a minute at a time before surfacing for air for less than a second, and according to surface conditions and the necessary remoteness of the observer might not be noticed. Curious gulls that circled above the sea-lion as it surfaced sometimes helped as intermediate observers. Towed coloured floats aided tracking for the observer but not for the sea-lion, which was slowed with extra work and sometimes distracted, and there was frequent fouling or breakage of the line. It was also proposed that for use in conjunction with aircraft patrols experiments should later be carried out to test the effect of colouring the head and back of a sea-lion with a vermilion grease paint for use by day or with a luminous paint for night. The floats themselves seemed a necessary measure, but the result of their use, together with a growing eagerness of

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[26] Paget, R.A.S. (23 April 1917) *Experiments with sea-lions on Lake Bala*; and Pleadwell, F.L. (24 April 1917) *Tracking and locating under-water sounds by means of the California sea-lion*. In Allen, E.J. (1917) ibid., note 6, appendices IV and V.

[27] Paget kept the Sub Committee informed of the latest developments at the meeting of 24 April 1917, and a report would be sent to the Director of the Anti-Submarine Department (PRO ADM 293/5, p.393).

the animals in the warmer weather to swim for enjoyment and not to respond to recalls, in spite of intensified food withdrawal incentives, led to a steady decline in reliability suggesting that in the open sea the animals might depart for good. Allen also gives a full account of the problems encountered when attempts were made to train a very nervous animal, 'Joffre,' who died within a few weeks in spite of the usual humane and sympathetic treatment. Other sea-lions, including further loans from the Zoological Society of London, displayed a variety of temperaments affecting training suitability. After sea trials in the first half of June, work at Lake Bala continued, until the conclusion of the whole programme in July, with a disappointing examination of the possibility of working with the animals without muzzles and a comparison of their hearing powers with those of a man using a naval-pattern hydrophone.

The sea trials themselves involved Billiken and Queenie at Gosport, in Stokes Bay and in the Solent between 30 May and 9 June 1917, when they were given the opportunity to chase submarine C15[28] for seven days and were reported on by Rear-Admiral R.A.Allenby on 11 June.[29] Surgeon Pleadwell took part in the final day's observations. The performance of the animals was very inconsistent and they showed a tendency to abscond. The greatest distance from which they managed to track C15 when submerged (but making extra noise) was 200 yards. Allenby paid tribute to Woodward's training and patience but said that Surgeon Pleadwell agreed with his view that the animals were not likely to be of any practical use and that they should 'return to their legitimate business' (by which he probably meant the circus and music hall rather than life in the wild).[30] These trials were a crucial point in the programme, coming also after a decline in controlled performance by the animals at Lake Bala, although Allen did not attend. Woodward informed him of the results, which showed ready distraction in these timid animals from extraneous sounds and sights,[31] the general influence of the hot weather which seemed to encourage the animals to stay in the water and not do very much, and in Billiken's case the negative effect of some bad herrings. The return to salt water may also have had an effect. However, Allen thought

[28]C15 was appropriately commanded by Lieutenant Dolphin.
[29]Allenby, R.A. (1917) *Use of sea-lions for submarine tracking*. In: Allen, E.J. (1917) ibid., note 6, appendix VI.
[30]Paget informed the Sub Committee on 20 June 1917 that the experimental programme was in abeyance in view of Allenby's advice to the Admiralty that the trials at Gosport raised no hopes of success under sea conditions. He added that the Central Committee of the BIR had agreed to ask for a further report from 'Captain' Woodward, who was not satisfied that in these trials the conditions allowed conclusive assessment; but Woodward's later submission failed to sustain the programme (PRO ADM 293/5, p.431).
[31]At Lake Bala, an old sea-lion, 'Dorando,' had continued to perform well and this was attributed to his failing eyesight and hearing. In a harsher experimental environment it might have been suggested that a deliberate impairment of the animals would improve their performance.

that with time some of these problems could be overcome, and at least during more than a week of open sea trials the animals remained under control and were not lost. More problematic was the supposed inability of the sea-lions to detect at distance in the open sea the feeble sounds of a stationary or slow-moving submarine, and, given their average tracking speed of about 5 mph, they would not be able to overtake a noisier, faster vessel.

In his final report, Allen made some 'suggestions in case of further experiments' which referred to the dependence on the food incentive and more acceptable 'off-duty' accommodation for training and for ensuring the reliability of recall which would be so essential in active service. The amount of food used had been the minimum considered necessary for good health, but it was suggested that a plan be tried of working the animals on alternate days, giving them little or no food on the idle days but doubling their rewards for successful work. It was in questions such as this that the advice of the circus trainer could have been augmented if not replaced by the information currently being derived from the development of laboratory-based behavioural studies by animal psychologists almost entirely in the United States.[32] Land-based training in obedience to orders was also recommended, but at no point was punishment as opposed to reward discussed as an alternative incentive. Finally, sounds for response should be confined to a recall signal and a submarine sound, and discerned from others from a variety of under-water directions. Once the recall signal had been learnt, training should continue with an actual submarine.

Seagulls

The Admiralty and the Board of Invention and Research had received suggestions to train gulls to detect periscopes in 1915 but the matter was not taken further until raised again and referred to the Director of the Anti-Submarine Department in late 1916. It was proposed that merchant ships should tow a dummy periscope 'from which at intervals food would be discharged like sausage-meat from a machine' to teach the birds to associate periscopes near ships with food, leading them to swoop on the periscopes of real submarines. Dr Chalmers Mitchell and Sir Charles Parsons of the Central Committee of the BIR were keen to try the scheme, but Admiral Duff was concerned that it could result in many scares.[33] Commodore Hall told the Sub

[32] Surgeon Pleadwell made no reference to these in the report of his observations.
[33] Memorandum of the Meeting of the Sub Committee of Section II, held on Tuesday January 9th 1917, PRO ADM 293/5, p.391. Parsons referred to the similar manner in which gamekeepers locate

Committee that the idea had often been considered and that in the previous autumn he had been instructed to prepare plans for the occasional discharge of fish from the torpedo tube of a submarine to ascertain bird attentiveness, but the matter had not been progressed. He felt it might be difficult to imitate the true appearance and steady movement of a periscope, and that captains might come to rely too much on gulls, the watch kept on merchant ships being in any case 'very bad'. Another commentator also pointed out that gulls are not found very far out at sea. However, the Sub Committee decided that a trial feeding mechanism should be devised.

At the meeting of the Central Committee of the Board of Invention and Research on 10 May 1917, presided over by Lord Fisher, it was reported: 'In consequence of a suggestion made by the Board of Invention and Research to test the possibilities of attracting seagulls to the periscopes of submarines by ejecting food therefrom and thereby training them to follow and locate enemy submarines, the Admiralty have approved an experiment being made in [submarine] B3 and have asked BIR to provide a suitable food box for the purpose'.[34] During the Sub Committee meeting of 22 May 1917,[35] Paget as secretary reported that a Mr Carnegie was constructing the apparatus for use with B3 in trials in the Firth of Forth. W.H.Hudson, the ornithologist and popular nature essayist,[36] had been invited to assist in the experiments. At this meeting the idea of using pigeons was raised: a ship could carry and control these birds. Commander Middleton who was present added that he had had experience with pigeons on board and that they would fly around at great distances. Paget replied that this idea had been put forward before, but that the officer in charge of the Whale Island pigeon loft had not considered it feasible. Middleton was asked to discuss the suitability of this and other species of birds with Hudson. Soon after, at the meeting of 19 June 1917, Paget reported that a falconer had suggested the use of hawks, but after later discussions with him the idea was considered impracticable.[37]

The approved programme of experiments was short-lived, and on 7 August 1917 the Sub Committee learned of difficulties that had arisen with the use of submarine B3. After making reference to the Admiralty, the Third Sea Lord soon decided that the experiments should be dropped altogether.[38] This was acknowledged at the meeting of

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vermin by observing the movement of birds.

[34]PRO ADM 293/7.

[35]PRO ADM 293/5, p.413.

[36]Hudson is assessed in Allen, D.E. (1994) *The naturalist in Britain: a social history*. 2nd ed. New Jersey: Princeton University Press, pp.206-7 & 210.

[37]PRO ADM 293/5, p.424.

[38]PRO ADM 293/5, p.444.

the Central Committee on 30 August, when it was noted that Richard Kearton, whose services had been obtained, had been informed accordingly and thanked.[39]

The development of ethology, and relations with animal psychology

The situation before the Second World War

Of the work that took place outside the laboratory before the Second World War, the best began to supply evidence that would help to create the emerging science of ethology. Crook[40] notes two opposed themes in the interpretation of animal social behaviour in the early part of the century: firstly, comparative anatomical and physiological zoology based on laboratory research including Mendelian perspectives versus, secondly, comparative social behaviour in whole-animal field studies[41] - often with a focus on populations or societies as processes within which individuals interact in systematic ways - and Julian Huxley's fresh Darwinian approach.

The scope of ethology at the beginning of the century was unclear, as was its meaning. This is apparent from the references to ethology in the *Zoological Record*. Much of the early work of relevance was ornithological, and carried out by wealthy amateurs who produced expensive publications with limited circulations. Such was Eliot Howard who lived a double life as a businessman and as a scientist who carried out the most painstaking and valuable observations on bird behaviour, resulting in, for example, the monograph *The British warblers* (1907-1914). 'His most enduring contribution to science was his emphasis on the important role played by the feeding territory round the nest in determining bird behaviour.[42] In his later books he became increasingly preoccupied with the theoretical and philosophical implications of his studies.'[43]

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[39]PRO ADM 293/7. A brief account of the eccentric Kearton brothers, who promoted bird photography and developed bizarre camouflage and hides for bird watchers, can be found in D.E.Allen (1994) ibid., p.211.
[40]Crook, J.H. (1989) Introduction: socioecological paradigms, evolution and history: perspectives for the 1990s. In: Standen, V. and Foley, R.A. (eds) (1989) *Comparative socioecology: the behavioural ecology of humans and other mammals*. Oxford: Blackwell, pp.4 & 5.
[41]e.g. Howard, H.E. (1920) *Territory in bird life*. London: Murray.
[42]Howard, H.E. (1920) op. cit.
[43]Douglas, J.W.B. and Zuckerman, S. (1941) Obituary: Mr Eliot Howard. *Bulletin of Animal Behaviour*, I, 3: iii.

The work of Howard was introduced to Lloyd Morgan by W.P.Pycraft,[44] who had written from the British Museum (Natural History) requesting of Lloyd Morgan a paper on instinct in birds for *British Birds*, of which Pycraft was sub-editor. Pycraft hoped that such a paper would help ornithologists to observe and understand objectively and without anthropomorphism, and also interest readers 'in some other channel than that of killing - by way of a change!'[45] He remarked that Howard was an admirer of Lloyd Morgan's work and Pycraft commended *The British Warblers*, describing Howard as one who had accumulated more knowledge than any other ornithologist in the country. By 1912 Lloyd Morgan had made contact with Howard, having asked him to let him know of any behaviour to which he thought Lloyd Morgan's theory of organic selection might apply. Howard[46] sent his observations, and their correspondence then continued on a regular basis until Lloyd Morgan's death in 1934, including exchanged visits and comments on each other's publications: a strong friendship developed, as between Howard and Julian Huxley. Meanwhile Pycraft[47] sought critical approval from both Lloyd Morgan and Hobhouse of the manuscript for his forthcoming book on *The courtship of animals*,[48] and thereafter remained in occasional contact with Lloyd Morgan until the 1930s, supplying information on the anecdotes of others and colourful details of his own apparently exhausting and hectic working life.[49]

The conditions under which ethology began to emerge in Great Britain included the development of interest in 'useful' behaviour in the natural environment, the basing of the interpretation of animal behaviour on careful preliminary description, extending interest to a fuller range of animals (especially birds, fish and insects) and behaviours, comparing similar behaviour in closely related species, and relying on wild rather than domesticated animals for all such evidence. This contrasted with the wish of the animal psychologist to look for truly general laws of behaviour by minimizing the role of the species-type and its habitat, for which various descriptive studies were therefore superfluous, and concentrating largely on the domesticated laboratory rat. Ethology as studied by field-orientated zoologists continued to make use of Darwinian

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[44]Pycraft, W.P. (1908a) Letter to C.Lloyd Morgan, 8 April. Bristol University History Collection, DM 128/179.
[45]Pycraft, W.P. (1908b) Letter to C.Lloyd Morgan, 28 November. Bristol University History Collection, DM 128/181.
[46]Howard, H.E. (1912) Letter to C.Lloyd Morgan, 24 August. Bristol University History Collection, DM 128/262.
[47]Pycraft, W.P. (1913a) Letter to C.Lloyd Morgan, 26 August. Bristol University History Collection, DM 128/289.
[48]Pycraft, W.P. (1913b) *The courtship of animals*. London: Hutchinson & Co.
[49]Pycraft, W.P. (1931) Letter to C.Lloyd Morgan, 3 January. Bristol University History Collection, DM 128/467.

evolutionary theories, while a concentration on environmental conditioning and learning processes led animal psychologists increasingly to neglect them, relying instead on the control of immediate variables and statistical analysis.

From 1900 to 1930, ethology was in its formative phase in Britain; and from the 1930s to the 1950s was the classical phase, dominated by the powerful school of Konrad Lorenz and Niko Tinbergen, and preoccupied with analyses of the adaptive significance, evolution, motivational and mechanistic control of innate behaviour patterns.[50] Edmund Selous (1858-1934) had been a particularly systematic ornithologist and influenced E.S.Armstrong, H.E.Howard, J.S.Huxley and F.B.Kirkman. After the First World War, Julian Huxley began simple but critical field studies to obtain data fundamental in the construction of a Darwinian natural history in which selectionist principles played the prime role in behavioural interpretation.[51] Crook[52] believes that 'Huxley's attempts to explain the mating system of birds in terms of ecological adaptation through natural selection were perhaps the first researches in which the principles of contemporary socioecology begin to come into view'.

F.B.Kirkman said of his own activities: 'Wherever it seemed possible and profitable, I supplemented observational work by experimental, well aware, however, that experiments in the field, though of undoubted value, cannot reach the quantitative precision of experiments in the laboratory'. He conducted field experiments which threw light on 'bird mentality, with special regard to the difference between the perceptual capacity of bird and bird or birds and men.'[53] His concern for attention to detail is revealed in a series of letters to Lloyd Morgan.[54] He noted that 'there is now a fairly large accumulation of fact about birds' habits and instincts, which no-one has utilised for purposes of the study of Animal Behaviour. I have fortunately been in a position to accumulate this material in the *British Bird Book* now in process of publication, of which I am editor and part author', and to which Pycraft contributed. Kirkman then gave detailed information on the nesting habits of the house-martin, which he thought had been inadequately described in Lloyd Morgan's *Animal*

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[50] Asquith, P.J. (1981) *Some aspects of anthropomorphism in the terminology and philosophy underlying Western and Japanese studies of the social behaviour of non-human primates*. Oxford University: unpublished D.Phil thesis; Crook, J.H. (1989) op. cit., p.5.
[51] Huxley, J.S. (1923) Courtship activities in the red-throated diver together with a discussion of the evolution of courtship in birds. *Journal of the Linnean Society*, 35: 253-92.
[52] (1989) op. cit., p.4.
[53] Kirkman, F.B. (1937) *Bird behaviour*. London: Nelson.
[54] Kirkman, F.B. (1912a, 1912b, 1913) Letters to C.Lloyd Morgan, 10 September, 13 November and early July. Bristol University History Collection. DM 128/265, 277 & 288.

Behaviour. He felt too that the chapter on sexual selection should have recognized sex displays in birds outwith the courtship period, and gives evidence for these, commenting 'birds having limited means of expression have often to make one gesture serve more than one purpose'. More information is supplied to add to that given in Lloyd Morgan's *Instinct and Experience*, as concerning the waterhen's use of its wings to swim under water.

At this time (1912) Kirkman was using Lloyd Morgan's books to deliver some Cambridge Extension Lantern Lectures on animal behaviour, which he found a 'prickly' subject, requiring Lloyd Morgan's later help over his difficulties in connection with Lloyd Morgan's theory of organic selection. He was to add that because he was not 'psychological enough, ... the whole question of the possible emergence in consciousness of the mental image is a thing I find it very hard to grasp', as proposed, for example, in imitative behaviour in cats in puzzle-boxes; but it was 'in the case of a bird ... stronger' although still doubtful. Kirkman offered Lloyd Morgan photographs and notes of cats which he had witnessed performing in puzzle-boxes, but believed little could be learned from them.

Of the *British Bird Book*, Kirkman shortly told Lloyd Morgan: 'If there is any species about which you wish information, I shall be very glad to send for your perusal the part containing it. I cannot present you the book, nor do I particularly recommend you to purchase it, as it costs, when complete, £6.6s, owing to the introduction into it of a number of more or less satisfactory colour plates, in not a few of which species so far unknown in nature have been created by the printers'. Kirkman explained his own motivation and purpose in bird study when he asked Lloyd Morgan: 'Could you recommend any periodical which makes a speciality of Animal Behaviour - from the Psychologist's point of view? The ornithological papers are useless for my purpose, except for facts. I know Thorndyke's [*sic*] work and the large bibliography in Washburne's book; also Stout's etc. My idea is to systematise our knowledge of Birds with a special eye to their value for the student of Animal Behaviour, as you understand it. My lectures are merely a preliminary canter in this direction'.

Kirkman[55] described to the British Association for the Advancement of Science his work on the black-headed gull, and served on a committee of the zoology and psychology sections to promote such work, and including J.S.Huxley, F.Aveling,

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[55]Kirkman, F.B. (1938) Recent field experiments on birds (1937-8). *British Association for the Advancement of Science: Reports*, Sectional Transactions - J, p.487.

C.S.Myers and E.S.Russell.[56] This was in line with what Selous would have wanted. He was a severe critic both of the experimental methods of purely laboratory-based psychologists and of the lack of analytical interest in behaviour among his fellow ornithologists. He wished to establish the study of the normal habits of birds on a secure foundation of detailed observation.[57] Huxley made some imaginative interpretations of courtship rituals in, for example, the great crested grebe, and spiced his observations with anthropomorphic sentiment, but without diminishing the value of his discoveries. F.H.A.Marshall, a lecturer in physiology at Cambridge, also began in the 1930s to interpret the sexual periodicity and the internal and external perceptual factors which govern it in birds. His discoveries had tremendous implications for ornithology,[58] since they revealed the effect of male display patterns on the sexual and reproductive behaviour of the female. He further examined the effect of cerebral electrical stimulation on ovulation in rabbits, noting whether there were any resulting follicles on the ovaries and whether or not ovulation occurred after the administration of three, three-second shocks of 30 volts with seven-second intervals, repeated once more at approximately the same time on subsequent days. The results were inconsistent.[59]

Both Huxley and Kirkman were instrumental in the setting up of the Institute for the Study of Animal Behaviour in 1936. It was founded by a number of zoologists, naturalists, physiologists and psychologists (including G.C.Grindley and David Katz), 'with the object of promoting and encouraging research into animal behaviour'. The Institute intended to act as a clearing house for information regarding work that was being done on animal behaviour in all its aspects 'and to bring together for the discussion of their problems field and laboratory workers ... Meetings for the transaction of scientific business will be held at monthly intervals'. The Institute hoped eventually to support research. R.C.Oldfield was the first Honorary Secretary.[60]

Bartlett[61] had recognized the restrictive shortcomings inherent in much purely laboratory work in an address to Section J of the British Association for the Advancement of Science:

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[56] *Reports*, 1940, p.370.
[57] Asquith, P.J. (1981) op. cit., p.56.
[58] Thorpe, W.H. (1979) *The origins and rise of ethology: the science of the natural behaviour of animals*. London: Heinemann, p.34.
[59] *Rabbits. Electrical Stimuli and Injection Experiments. Dr Marshall and Dr Verney.* Notebook, c.1937-1939. Cambridge Univ Lib. MS Room. Add. 9216/3.
[60] *British Journal of Psychology*, 1936, vol. XXVII, part 2.
[61] Bartlett, F.C. (1929) Presidential address. Experimental method in psychology. *British Association for the Advancement of Science: Reports*, Section J, pp.186-98.

> If the psychologist is asked to point out any single unshakable discovery of first- rate psychological importance, based directly and wholly upon experiment, his attempts to answer the question are always regarded as unsatisfactory ... The earliest experimentalists in psychology were physicists and physiologists ... They set up a standard which in various ways has cramped and confined experimental psychology ever since. When a physicist approaches a problem in which he has to state how a stimulus affects any kind of response, he is bound to lay the burden of explanation upon the stimulus.

The psychologist 'must not stand in awe of the stimulus' and ignore conditions of response which belong to the subjective attitude, to predetermined reaction tendencies and to temperament and character.[62]

In his presidential address to Section D (Zoology) in 1934, E.S.Russell agreed with an earlier claim by James Gray that 'the conception of the organism as a single living entity is or should be the more peculiar attribute of experimental biology'.[63] In the previous year,[64] he had written to Lloyd Morgan:

> In objective plain tale description we do not need to separate body-story from mind-story; would it not be possible to develop 'plain tale' into an organismic behaviourism, simply recording what the animal does, and by simple experiment deducing what its perceptual world must be? I feel that behaviour is so intimately connected with morphogenetic and physiological processes - notably in reproductive behaviour - that one must somehow contrive to treat them all together, at least to begin with. One can analyse afterwards, and thus work down to physiology, but the results so obtained by study of the parts of the whole-action cannot supersede or be substituted for the broad plain tale generalisations obtained by study of the activities of the whole intact animal ... I find the only satisfactory way to treat the subject in an elementary way is to avoid both psychology and physiology and in effect limit oneself to plain tale. After all, a good deal of modern work, such as that by Kohler and Bierens de Haan and - so far as I can see from a glance at his new book - Kluver also goes little beyond plain tale ... Animal behaviour is a subject which has always interested me, especially in its ecological or natural history aspect, and I hope soon to be able to devote myself entirely to it. I have not had time to do much

[62]Bartlett, F.C. (1932) *Remembering: a study in experimental and social psychology*. Cambridge: University Press. Cited by Joynson, R.B. (1970) in: The breakdown of modern psychology. *Bulletin of the British Psychological Society*, 23: 261-9.
[63]Russell, E.S. (1934a) Presidential address. The study of behaviour. *British Association for the Advancement of Science: Reports*, Section D, pp.83-98.
[64]Russell, E.S. (1933) Letter to C.Lloyd Morgan, 29 October. Bristol University History Collection, DM 612.

> in a practical way so far, but hope to publish an elementary book on the subject in the spring.

Key British resistors to behaviourism and the laboratory emphasis continued in Russell and Huxley, both of whom also contributed to the development of a sympathetic climate for the rise of ethology. Russell saw limitations in behaviourist, mechanistic and reflex theories, and in the causal-analytic method, as applied to studies in animal behaviour. On the contrary, he believed that animals were perceptive and that they exhibited directive activity, largely for the purpose of self-maintenance in the natural environment. Like Julian Huxley, he experimented, but he was not prepared to be bound by the dogma of a new scientific psychology as propagated in the United States of America. Russell and Huxley were prominent scientists and also popularizers of science, and their influence must have been great both among those professionally interested in comparative psychology and among the public whose attention was increasingly being drawn to such problems of science and natural history by the development of popular publications and the range of coverage of broadcast media and film. Russell continued the kind of scepticism Hobhouse showed towards Thorndike's work. He was interested in the behaviour of animals rather than in those laws of learning which might be shared between animals and humans, as studied by many laboratory animal psychologists, who were not so interested in animal behaviour *per se* and therefore studied a sort of applied psychology. However, Russell's interests also had applied value, for example those concerning fish migrations as related to ecological conditions.

Solly Zuckerman was critical of the contents of Russell's presidential speech of 1934. He took the objectivist stance and warned:

> The reintroduction of the terminology of introspective psychology would be a disastrous step, calculated only to return the subject to its discredited anthropomorphic and anecdotal phase. The study of animal behaviour should be allowed to proceed, and animal behaviour should continue to be interpreted, by the one method that gives certain knowledge - namely, by the application of well-established scientific method to objectively definable data, data which can be stated without the fear of ambiguity.[65]

Russell, on the other hand, complained that

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[65]Zuckerman, S. (1934) The interpretation of animal behaviour. *Science Progress*, 29: 639-49. (From a paper contributed to the discussion of the subject by Sections D and H, British Association for the Advancement of Science, at the Aberdeen meeting of September 1934.)

> ... the study of animal behaviour has been largely divorced from the general study of zoology, and handed over to the physiologist and the psychologist, neither of whom is, as a rule, sufficient of a naturalist to appreciate the full biological significance of the behaviour observed in the laboratory. It is of course obvious that an animal's behaviour is one of the most important things about it, and if the zoologist wishes to understand how his animal lives, maintains itself, and carries on the race, the first thing he should study is its behaviour in the field. It is also clear that a thorough knowledge of the bionomics or ecology of the animal is quite essential for the interpretation of its behaviour in the experimental conditions of the laboratory.

Russell's *The behaviour of animals: an introduction to its study* (1934) was based on his 1933 lectures in the Department of Zoology and Comparative Anatomy at University College, London. The new book contained much observational and experimental material, with an emphasis on instinctive behaviour and on perceptual aspects of instinct: 'the emphasis on the ecological and "natural history" aspect of behaviour is apt to be overlooked by the laboratory worker'. Now thanking Lloyd Morgan for his appreciation of his book, Russell[66] wrote that 'the tendency among zoologists is still to treat behaviour as physiology, without paying sufficient attention to ecological background and "natural history". I am trying to combat that attitude, and the "laboratory mind", in my book, while at the same time appealing to non-professional readers ...' and[67] '... the great number of people who are interested in what animals do and how they live'.

Scientific, philosophical and historical objections to the unsatisfactory study of animal behaviour were expressed in Russell's presidential address of 1934, which deserves the quotation of an extended excerpt:

> While excellent work in the field of scientific natural history is being done by the animal ecologist, the economic entomologist, the fishery worker and also by the amateur naturalist, they have not as a rule taken what one might call a professional interest in the problems of animal behaviour, though they have accumulated a great store of observations which are of the highest value to the professional student ... Generally speaking, as things are at present, the study of animal behaviour as a science has not in this country taken its rightful place as an essential part of zoology, either in research or in teaching; the tendency has been to treat it either as a branch of physiology or as an adjunct to

[66]Russell, E.S. (1934c) Letter to C.Lloyd Morgan, 8 April. Bristol University History Collection, DM 128/532.

[67]Russell, E.S. (1934b) *The behaviour of animals: an introduction to its study*. London: Arnold, pp.v & vi.

psychology, and in both cases to turn it into a laboratory subject ... The physiologist as such can have nothing to do with mind, and hands over its study to the psychologist, who finds that he can know nothing directly about the minds of animals. Hence ... the study of animal behaviour split up between physiology and psychology, with no possibility of a connecting bridge. The scientific study of behaviour thus becomes divorced from natural history and ceases to take its rightful place as an integral part of zoology ... [In a dog there is] definite evidence of memory, or retentiveness ... there is abundant evidence that animals perceive their surroundings ... and react to an external world of their own; here, as in our own case, perception may be regarded as a function of organism, not of 'mind' ... This is essentially the attitude of ordinary common sense. In practice we treat our fellow men and at least the higher animals as being real individuals with perceptions, feelings, desires, similar to our own. And common sense is in principle justified, though of course it runs a great risk of reading human motives, human ways of thought, into the behaviour of animals, and of assuming without sufficient warrant that their perceptual worlds are the same as ours. But because there is a danger of faulty interpretation, due mainly to inaccurate or inadequate observation, we are not thereby compelled to throw over the general conception that the animal organism is capable of perception, conative behaviour, and memory, if the facts of observation lead us to this conclusion ... behaviour is an activity of the organism as an intact and unitary whole ... by taking the parts in isolation, we abstract from their relations to the whole, particularly their temporal relations, and we leave out of account just what is fundamentally important - the working together of all the parts in the directive activities of self-maintenance, development and reproduction ... The plain tale description of animal behaviour must begin with a study of the natural history and ecology of the animal ... the general rule of biological method [is] that the whole life-cycle of activity must be regarded as the primary thing, and that the parts of it which may be isolated for study must be re-integrated in the whole-activity ... [The] analytical and physiological view is a pure hypothesis, derivable from the Cartesian metaphysics, and ... it does not harmonise well with the simplest facts of observation ... Nothing is more striking than the apparent spontaneity of animal actions ... the forces that produce instinctive activities are not in the stimulus-situation - they are within the organism itself ... A very great part of the behaviour of animals is, quite simply, response to needs (or deviations from normal), and not to direct external stimulation ... the broad fact remains that it is lack of normality, or the absence of some condition necessary for maintenance or development or reproduction, that sets much of behaviour going ... This is the essence of the principle of Gestalt - response to elements in the perceptual field as parts of the pattern of the whole. The principle of the whole is thus valid for the perceptual field just as it is for executive behaviour.

Russell stressed the need for observation and recording in the field, and valued the publications of observers like R.W.G.Hingston,[68] who had graduated in medicine in 1910 and spent the next seventeen years with the Indian Medical Service. As an arachnologist in his spare time, Hingston took more interest in the behaviour than the classification or physiology of his subjects, for example examining the web-spinning process by experimentally cutting away chosen parts during construction to identify the spider's instinctive response: 'This work and more he described in a set of books of great interest, models in their way of the presentation of new scientific work in a form in which all general readers could appreciate and enjoy it'.[69]

Other relevant work by Russell himself was *The interpretation of development and heredity* (1930), *Detour experiments with sticklebacks* (1931), and *Conation and perception in animal learning* (1932). When the Institute for the Study of Animal Behaviour was established in 1936, Russell was based at the Ministry of Agriculture and Fisheries Laboratory at Lowestoft, but at the same time he held the post of Honorary Lecturer on Animal Behaviour at University College, London, and as such 'he was the only founder member of the Institute (and probably the only man in Britain) to hold an official university post in this subject.'[70]

By the time of the start of the Second World War, Russell had come to represent the most developed areas of the subject that would soon more generally be known as ethology. His co-ordinated treatment of the subject had developed significantly from the occasional forays into it in previous decades. There had been progressive observational work even by 1901, when J.A.Thomson delivered an illuminating report to the British Association entitled 'Some notes on the behaviour of young gulls artificially hatched'. He had collaborated with J.L.McIntyre, Lecturer on Comparative Psychology at Aberdeen, but he carried out most of the observation himself, making detailed records of the newly hatched birds as their behaviour developed into adulthood. He exchanged many friendly letters with Lloyd Morgan concerning publishing activities and reviews of each other's work.[71]

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[68]For example, (1928) *Problems of instinct and intelligence*. London: Macmillan.
[69]Savory, T.H. (1961) *Spiders, men and scorpions, being the history of arachnology*. London: University Press, p.97.
[70]Durant, J. (1986b) The making of ethology: the Association for the Study of Animal Behaviour, 1936 to 1986. *Animal Behaviour*, 34: 1604.
[71]e.g. Thomson, J.A. (1903, 1923) Letters to C.Lloyd Morgan, 13 March 1903 and 26 July 1923. Bristol University History Collection, DM 128/121 & 354.

In 1903, G.Leighton had described 'Some recent observations on British reptiles' to the British Association for the Advancement of Science, mentioning that investigations and experiment with adders in the Scottish Highlands proved that in that district adders were in the habit of swimming the streams and rivers - previously a matter of dispute. The British Association for the Advancement of Science reported that in 1908 Dr D.G.Thomson delivered 'Notes on a tame hare'.[72] Later, in 1925, A.H.H.Fraser (Kilgorn Scholar in Natural Science, University of Aberdeen) described 'Chain instincts in lambing sheep' from notes made while working as a lambing shepherd in 1923 in Berwickshire.[73] In the transactions of Section D for 1934 Dr F.Darling reported on observational field studies of a herd of Scottish Red Deer.[74] David Lack, also in the transactions of Section D, in 1938 dealt with bird courtship display and aggressive behaviour: observations were complemented by experiments using stuffed specimens, and the responses of robins were assessed.

Frances Pitt had published a number of popular and semi- learned books with an ethological slant: *Wild creatures of garden and hedgerow* (1920); *Animal mind* (1927); and *The intelligence of animals: studies in comparative psychology* (1931). Her observations were frequently cited by E.S.Russell.[75] Descriptions are given of subjects such as a hand-reared thrush's discovery of how to break snails, or the ability of a cat to act as mother to a rat. *Animal mind* is a collection of notes and original observations on animal behaviour, mainly that of wild animals, using 'accuracy and scientific exactness'. Pitt believed that animal thought rather than instinct lay behind much behaviour (except in the invertebrates), and that intelligence could easily be underestimated, as could 'personality', in the higher vertebrates, mammals and birds. Her later book of 1931 was, according to a reviewer,[76] a psycho-biological survey, but it also contained many anthropomorphic, even sentimental, ideas, including that of the survival value of temperament. Her assessments of animal mind are in sharp

[72] *Transactions of the Norfolk and Norwich Naturalists' Society*, 1908, viii: 540-6.
[73] Fraser, A.H.H. (1926) Chain instincts in lambing sheep. *British Journal of Psychology*, XVI: 311.
[74] 'Work upon such a species is likely to be fruitful in interpreting certain lines of animal behaviour, (*a*) because animals in the wild state seem to react differently on different occasions to similar sets of circumstances, which must mean that there are variables present of which we are, as yet, unaware; (*b*) because laboratory experiments on animal behaviour as pointers towards interpretation should only be conducted after a considerable knowledge has been gained of the animal's behaviour in freedom; and (*c*) because, as most animals are in some measure gregarious, their behaviour as individuals and as members of a group cannot be divorced, and there is much to be learnt about community life of which the individual life is only a part. Among the many aspects of the deer's life observed are the territorial seasons and their sharply differentiated characteristics, meteorological factors, biological factors, relation of the sexes to one another and the different behaviour of the sexes in the social structure of the community during the different seasons of the year' (p.324).
[75] e.g. 1934b op. cit.
[76] Thomson, J.A. (1932) Book review: Comparative psychology in the field. *Nature*, 129: 6-7.

contrast with those of Rex Knight, as also reported in *Nature* in 1932[77] and in *British Association for the Advancement of Science: Reports*, Sectional Transactions - D.[78]

In the 1937 conference of delegates from the corresponding societies of the British Association for the Advancement of Science, the continuing participation of the amateur in this area of growing public interest was encouraged, and simple outdoor experiments in experimental zoology, such as testing the intelligence of earthworms or discovering the reaction to colour of midges, were suggested. But regarded as more appropriate were observations such as those on the nesting activity or singing of common birds. Interest in the late 1930s in popular fitness, the 'outdoor movement', and in activities such as rambling, served such encouragement of amateur involvement. The emphasis was put now on studying and recording rather than interfering and collecting: 'Every egg taken destroys an opportunity of recording the development of the young, and that is what we wish to learn about, life and its development.'[79] E.S.Russell had also written:[80] 'It is far more important nowadays to work out the life-history and habits of a beetle or a caddis-fly than to form extensive collections or make new "records"'.

The situation after the Second World War

After the end of the Second World War, ethology was given encouragement by the Royal Society (1946) which reported: 'With the advance in biological knowledge it has become increasingly evident that fundamental research must be directed towards the study of living organisms and their relation with their natural surroundings. Such facilities as do exist for the study of living animals and plants under natural conditions deal almost only with marine and freshwater biology, and it is essential to develop opportunities for field research in terrestrial ecology in the widest sense'. Furthermore, in 1949 the Nature Conservancy was established under the directorship of 'a great pioneer in terrestrial animal ecology,'[81] Captain Cyril Driver, thus enabling field experimentation to flourish.

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[77]Knight, A.R. (1932b) The explanation of animal behaviour. *Nature*, 130: 649-51.
[78]1934, p.324.
[79]Ritchie, J. (1937) The outlook of natural history. *British Association for the Advancement of Science: Reports*, p.452.
[80](1934b) op. cit., p.vi.
[81]Hardy, A.C. (1949) Zoology outside the laboratory. *The Advancement of Science*, VI, 23: 213-23.

The post-war development of the Institute for the Study of Animal Behaviour, the enthusiastic work of its members and the assimilation into behavioural studies of influences from continental Europe resulted in the consolidation in Britain of ethology, which was at first characterized by a reaction against laboratory work. Two key figures in the establishment of ethology, Lorenz and Tinbergen, had not, apparently, used the term 'ethology' in any distinguishing sense and were unsure of its origins, but it came to be used as a designative association for their work as opposed to that conducted in what was thought to be the artificial laboratory situations of comparative psychology. There followed 'a period of partisanship in some quarters between comparative psychologists in psychology departments and ethologists in zoology departments that in the long run had a beneficial effect in exposing and correcting the theoretical excesses on both sides.'[82] The division that took place and which was replicated across the Atlantic in some cases remained[83] and has created confusion in the interpretation of the nature, meaning and proper study of animal behaviour. There has been a mixture of competition, amalgamation and 'sometimes an antipathy eroding truth into loyalty, and sometimes, fortunately, a division of labour benefiting all', but 'by the 1960s, most of this division of loyalties had diminished, and both psychologists and zoologists were getting back to the co-operative venture.'[84] Rex Knight summarized the concerns felt by some psychologists over ethological methods by posing three questions that had been suggested in a critique of ethological theory by D.Lehrman:[85] Is the ethologists' use of the comparative method sufficiently strict? Are the ethologists' criteria of innateness satisfactory? Are the ethologists on the wrong track in looking for unitary, autonomously-developing behaviour patterns?[86] Lehrman's mastery of original ethological source material in German enabled him to construct his critique all the more effectively, and although Tinbergen was by then at Oxford, many of his British students could not fully examine the early history of ethology because of the language barrier.[87]

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[82]Jaynes, J. (1969) The historical origins of 'Ethology' and 'Comparative Psychology'. *Animal Behaviour*, 17, p.605.
[83]For example, the ethologists J.H.Crook and J.D.Goss-Custard described comparative psychology as 'highly controlled experimental testing of a range of alternative learning theories and animal training methodologies which ... lack the breadth endowed by a firm base in biology' (1972. Social ethology. *Annual Review of Psychology* 23: 277-312).
[84]Jaynes, J. (1969) op. cit., pp.601 & 605.
[85]Lehrman, D. S. (1953) A critique of Konrad Lorenz's theory of instinctive behavior. *Quarterly Review of Biology*, 28: 337-63. Cited by Knight, A.R. (1955) in Animal behaviour. *The Advancement of Science*, XII, 45: 17-27.
[86]Knight, A.R. (1955) ibid.
[87]Gottlieb G. (1979) Comparative psychology and ethology. In: Hearst, E. (ed.) (1979) *The first century of experimental psychology*. Hillsdale, New Jersey: Lawrence Erlbaum Associates, p.165.

But ethology indeed won over some converts from work that was purely laboratory-based. Kurt Danziger was at Oxford from 1949 to 1951, working on a D.Phil. thesis which was based entirely on animal work in the laboratory:

> During that period the influence of one or two people outside psychology was very much more important than anything within the discipline ... Tinbergen's presence at Oxford was a major factor. For me personally Tinbergen was important, because he made me see the problems with the American animal work. By that time I was however locked into my D.Phil. project, and so this influence is not reflected in my publications. It simply meant that I soon gave up animal work altogether. Of course, ethology had a much more positive effect on others.[88]

Evidence for this positive effect is provided by the presence, side by side, of articles on both laboratory and field experiments and studies in the British journals of animal behaviour of the 1950s, and by references to and products of co-operation and collaboration. Sluckin[89] later wrote that imprinting 'is a field where there is much activity, and experimentation here is characterised by a merging of the ethological and comparative-psychological traditions ... research (on mother-infant interaction in monkeys) combines the ethological and psychological approaches'. In 1961, the collaboration of workers in the laboratory and the field, facilitated by the Behaviour Discussion Group of 1953-1958, resulted in the publication of open and positive interdisciplinary assessments of various types and methods of research in animal behaviour.[90] Nevertheless, Thorpe himself remained sceptical about comparative psychology.[91]

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[88]Danziger, K. (1987) Personal communication, 19 January.

[89]Sluckin, W. (1969) Animal behavioural and ethological work. *Supplement to the Bulletin of the British Psychological Society*, 22: 35-6.

[90]Thorpe, W.H. and Zangwill, O.L. (eds) (1961) *Current problems in animal behaviour*. Cambridge: University Press.

[91]Dewsbury, D.A. (1984) *Comparative psychology in the twentieth century*. Stroudsburg, Pennsylvania: Hutchinson Ross, p.16, cites the following examples. '[The psychologist] has worked mainly with mammals - above all the white rat - and has devoted but little attention to interspecies differences or to the significance of his findings for behaviour in its natural setting. Indeed one may surmise that the psychologist has chosen to work with animals rather than with men largely on account of their lesser complexity and greater tolerance of the indignities of the experiment!' (Thorpe, W.H. and Zangwill, O.L., 1961, op. cit., p.x). 'Psychology tended to treat animals as if they were tiny men and so was subjective in approach.' (Thorpe, W.H., 1979, op. cit., p.ix). 'Comparative psychology, on the other hand, as the term has been used for the past fifty years or so, seems (temporarily one hopes) to have lost its identity and be on the wane.' (Thorpe, W.H., 1979, ibid., p.166). Thorpe also entitled a paper: 'Is there a comparative psychology? The relevance of inherited and acquired constraints in the action patterns and perceptions of animals'. (*Annals of the New York Academy of Sciences* 223: 89-112).

While comparative psychology stresses the laboratory investigation of perception and learning in animals and man, ethology studies the evolution of the relatively stereotyped and instinctive behaviour patterns of animals in their natural environment. Thorpe[92] describes Darwin as a forerunner of modern ethology, for in his *Expression of the emotions in man and animals* 'he is concerned not so much with the emotions as they are supposed to be felt by the animal (though this is implied) but with the similarities of emotional expression and behaviour in widely separated groups of animals'. Ethology was founded upon naturalistic observation of emotions and physical attitudes that were as much species' characteristics as colours or structures. The concept of 'gesture' was thus very important as a classification unit. As comparative psychologists struggled to be objective, the ethologists adopted methods based on the observer's personal insight, although Tinbergen[93] later wished to achieve objectivity through the incorporation of experiment in observation.[94] The early systematic observations of ornithologists like Edmund Selous and of Julian Huxley had been influential before the Second World War, and these influences affected workers like Thorpe and Lack after it, too. However, the term 'ethology' in its post-war sense was not used in Britain before the 1940s, as can be realized from its vague use for classification in the *Zoological Record*, and, as mentioned above, natural behaviour studies had in any case been restricted mainly to wealthy amateurs who occasionally produced expensive publications for limited circulation. For these reasons, the development of what became known as ethology was intermittent in Britain before the war, while more positive establishment of the new method took place in Austria, Germany and Holland.[95]

Before examining the details of the introduction of ethological work into Britain it may be useful to consider the recent definitions and descriptions of ethology made by scientists over the past twenty years, since their interpretations have been drawn up with an eye to its rapid rise alongside laboratory-based animal psychology. Green[96] claims that much of what is now known about animal behaviour comes from an approach quite different from that of the comparative psychologists, because ethologists have discovered how an animal's behaviour contributes to its ability to survive and reproduce in its habitat while dealing with members of its own and other

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[92]Thorpe, W.H. (1956) Some implications of the study of animal behaviour. *The Advancement of Science*, XIII, 50: 42-55.
[93]Tinbergen, N. (1942) The objectivist study of the innate behaviour of animals. *Bibliotheca Biotheoretica*, 1: 39-98; (1951) *The study of instinct*. Oxford: University Press.
[94]Asquith, P.J. (1981) op. cit., pp.38, 71 & 72.
[95]Asquith, P.J. (1981) op. cit., pp.50-1.
[96]Green, P. (1981) Animal psychology. In: Gillham, B. (ed.) (1981) *Psychology for today*. London: Hodder and Stoughton, pp.159-72.

species. The behaviour patterns studied (e.g. those of sticklebacks by Tinbergen, 1951) seemed to be the same in all members of a species and to appear without any learning. Thus arose the nature-nurture controversy, as comparative psychologists emphasized their continued belief in the role of conditioning in the creation of learned responses. Studies of 'imprinting' in young precocial birds added to the debate; and the importance of learning was also claimed to be more relevant in the higher animals: the higher up the evolutionary scale a species had developed, the less was its dependence on innate behaviour and the more its susceptibilty to environmental conditioning and adaptation. Comparative psychologists began better to appreciate the importance of evolutionary and functional situations as a result of ethological work, but for their part ethologists began to realize that some behaviour could be studied only under controlled conditions and that quantitative methods could lend greater precision to their data.[97]

Ethology is concerned with preliminary descriptions of observable behaviour as an indispensable basis for the formulation of problems concerning not just man, the rat and a few other mammals as usually favoured as subjects by psychologists. Total behaviour patterns interest the ethologist, who aims at a balanced study centred not only on causation but also on survival value and evolution, factors neglected by psychology.[98] Attention is given by the ethologist to healthy, undamaged animals, while the psychologist may study sick and injured animals in specially contrived and extraordinary laboratory situations. Ethology regards instinctive activities as quite rigid and therefore entitled to taxonomic categorization like morphological characteristics, although these activities may sometimes be pliable in 'appetitive' as opposed to 'consummatory' behaviour, but without the plasticity of learning, which has the greatest relevance for the psychologist.[99] Ethological research has shown that human benefit from animal studies must in some respects be limited, because of the existence of species-specific behaviour, although there are certain features about the central nervous system which appear to cross species. Just as ducks and geese share similar skeletons, so their behaviour is similar, and these similarities, as between other groups of animals, set them apart. Similarities and differences are governed by the environment, food-gathering and predator threats, and Tinbergen[100] illustrated resulting patterns of behaviour in the example of greylag geese. Stereotyped behaviour

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[97]Dewsbury, D.A. and Rethlingshafer (eds) (1974) *Comparative psychology: a modern survey.* Tokyo: McGraw-Hill Kogakusha Ltd, p.11.
[98]Tinbergen, N. (1955) op. cit.
[99]Hediger, H. (1972) Animal psychology. In: Eysenck, H.J., Arnold, W. and Meili, R. (eds) (1972) *Encyclopaedia of psychology* Vol.1. London: Search Press.
[100]Tinbergen, N. (1951) op. cit.

patterns, which become known as 'fixed action patterns' are characterized by stereotypy, universality, independence of individual experience, ballisticness, singleness of purpose and the existence of known trigger stimuli.[101] Behaviour would occur along predictable lines by virtue of inherent 'drives' in the animal which would be built up periodically and then satisfied by the effect of particular external stimuli on the 'innate releasing mechanism' (- this describes 'instinctive behaviour' but does not, however, explain it). In drive-conflict situations, 'displacement reactions' might occur, and incidentally serve as a form of communication between animals which has sometimes evolved into ritualization in its own right, able to be elicited independently by a totally different, single stimulus, as in courtship posturing. It is suggested that behaviour like this can be influenced by genetic factors and that it demonstrates the inheritance of instincts alongside phenomena like visible markings and species-audible signals.[102]

Although some comparative psychologists and ethologists failed still to communicate adequately in the conduct of their research, interaction increased during the 1950s and 1960s. Ethologists have published papers in the *Journal of Comparative and Physiological Psychology* and psychologists have done so in *Behaviour*, *Animal Behaviour* and the *Zeitschrift fur Tierpsychologie*.[103] In 1969 Hearnshaw was able to report: 'That the situation today in the field of comparative psychology is again much brighter is a result largely of a blood transfusion from continental ethology, which has led to a renewed interest in animal behaviour, and a reforging of the links between psychologists and zoologists.'[104] Tinbergen himself was ready to confirm this view as the links became stronger:

> But now you can't really talk about ethologists any more. We learnt a great deal from the American psychologists who criticized us and they also came to see the value of the sort of evidence we had. Now, for example, you have two zoologists teaching here at the Institute of Experimental Psychology [in Oxford] and plenty of psychologists have developed an interest in animals other than the white rat. There's been mutual traffic ... many psychology departments now employ zoologists on their staff. Here in Oxford zoology and psychology share the same building.

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[101] Lea, S.E.G. (1984) *Instinct, environment and behaviour*. London: Methuen, pp.13, 19 & 21-23.
[102] ibid., pp. 31 & 36-43.
[103] Dewsbury, D.A. and Rethlingshafer, D.A. (eds) (1974) op. cit., pp.11 & 12.
[104] Hearnshaw, L.S. (1969) Psychology in Great Britain: an introductory historical essay. *Supplement to the Bulletin of the British Psychological Society*, 22: 3-9.

He revealed, too, a strong attraction to the laboratory: experimental work 'is still the work I love most ... My interest in an animal intensifies at once when I see it in its own environment ... yet I don't regret at all the time spent in laboratory studies.'[105]

The development of ethology in Britain was closely connected with the formation of the Institute for the Study of Animal Behaviour and the subsequent activities of some of its members,[106] but the encouragement of public interest in the natural observation of animals had already been established by writers with zoological or relevant scientific qualifications well before the outbreak of the Second World War,[107] and continued after its conclusion.[108] However, the scientific community itself had never had much regard for activities such as birdwatching, even if the observation was supposed to be analytical. In order to make field studies truly respectable, prominent advocates with impeccable scientific credentials were needed. These advocates appeared in the persons of Julian Huxley and Solly Zuckerman, both of whom had expectations for the future of animal behaviour. Huxley wanted to link field observations of birds to evolutionary theory and psychology, but Zuckerman was more interested in laboratory-based work in the experimental physiology of behaviour. Huxley explained the original motivation and inspiration for his work: 'Darwin's theory of evolution by natural selection had emerged as one of the great liberating concepts of science ... I resolved that all my scientific studies would be undertaken in a Darwinian spirit and that my major work would be concerned with evolution, in nature and in man ... I was always much more interested in the behaviour of living animals and their past evolution than in the physico-chemical basis of their activities'.[109] Later his interests developed to include, as director-general of UNESCO in 1946, the promotion of a better understanding of science, especially biology and psychology, by all nations, his three main interests by the 1950s consisting of over-population, conservation and evolution.[110]

While Huxley thought that ethological studies of animal behaviour could throw light on the human condition, Zuckerman felt very differently, and emphasized the inability

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[105]Cohen, D. (1977) *Psychologists on psychology*. London: Routledge & Kegan Paul, pp.318 & 325-7.
[106]But not with those of Solly Zuckerman, who was critical of ethology and ethologists.
[107]e.g. Pycraft, W.P. (1913b) op. cit.
[108]For example: Cloudsley-Thompson (1960), Cott (1940), Fisher (1940), Howard (1952), Knight (1957), Matthews & Knight (1963), Munro Fox (1940), Pitt (1920, 1927, 1931, 1938, 1940 & 1946), Shoosmith (1937), Stephenson (1946). Full details of the work of these authors appear in the Bibliography.
[109]Huxley, J.S. (1970) *Memories*, vol.1. London: George Allen and Unwin Ltd, pp.73 & 96.
[110]Ibid., vol.2, pp.15ff & 181.

either of early comparative psychology or of ethology to do this: 'Re-reading my article[111] I can also see that my unbending critical attitude to attempts to explain human behaviour by analogies from the animal world must have been acquired at a very early age'. He referred to Konrad Lorenz, Desmond Morris and Robert Ardrey as three later writers equally adept at devising superficial analogies,[112] but perhaps in deference to a closer associate failed to criticize Huxley[113] who in 1965 had arranged a Royal Society conference on the ritualization of behaviour in animals and man. The conference included Desmond Morris on 'forced movement' rituals in captive animals, and the rigidification of their behaviour. Huxley believed that the conference helped to establish that the study of animal behaviour was relevant to human affairs.[114] Lorenz's

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[111]In *The Realist*, 1929, 1: 72-88, *The social life of the primates*. He wrote: 'Until recently, the study of animal psychology was pursued mainly in order to obtain evidence supporting the Darwinian hypothesis by demonstrating mental continuity between the animal and human worlds. Its point of view, however, was anthropomorphic, and its extravagant exposition provided some animals with an intelligence little less than human and many with a code of morals which would have sustained them in any civilized community. From this plight it was rescued at the beginning of the present century, and today [1929] the study of animal behaviour is one of the more stimulating and useful branches of psychology. On the other hand, animal sociology stands today where animal psychology stood thirty years ago. Its method is still mainly anthropomorphic description, either in the older blatant form or in a new guise, provided with a crude behaviouristic formula which explains all behaviour as the product of an instinctive nucleus and experience. In the hands of its exponents animals share with man a common classificatory scheme of social conduct. However sound this formula may be, one can see in it no justification for such purely speculative assumptions as those made by Alverdes in maintaining that human monogamy and the monogamy of birds are comparable, and can be discussed in comparable terms'.

[112]Zuckerman, S. (1978) *From apes to warlords: an autobiography 1904-46*. London: Hamish Hamilton, pp.41-42.

[113]But in 1987 Zuckerman set out to qualify Huxley's role: 'He was not interested in (at least he never referred to) the analytical studies of behaviour ... [Concerning his] having founded an Institute for the Study of Animal Behaviour. The fact is that no such institute was ever founded. There was never a hope that it would be, and Julian never set out a plan to show what such an institute might do ... Apart from a few studies of animal behaviour that I had started in Oxford, in those days the only other group working on the subject in the United Kingdom were members of a single department at Cambridge. In the whole country there was no proper facility where careful studies of animal behaviour could be carried out. Since Julian was then secretary of the Zoological Society, the idea was that we would create a facility in the London zoo where we could carry out truly scientific studies of animal behaviour. I arranged for two of my pupils to work there and to carry out experiments based on the idea that animal behaviour could be dealt with objectively and not in terms of parallels with human behaviour [and to determine whether numerical abstractions were unique to the human mind] ... That was all there was to the so-called "Institute of Animal Behaviour." Julian was interested in my experiment, but he did not build an "Institute" in the London Zoological Gardens'. These rather dismissive, if not possessive, comments may reflect Zuckerman's clear hostility to any work affected by anthropomorphism: the founders of the Institute obviously had incompatible approaches to animal behaviour, either realized at the time or in retrospect (Zuckerman, S., Comments and recollections, in Waters, C.K. and Van Helden A., eds, 1992, *Julian Huxley - biologist and statesman of science. Proceedings of a conference held at Rice University, 25-27 September 1987*. Houston, Texas: Rice University Press, pp.163-4).

[114]Huxley, J.S. (1970) op. cit., vol.2, p.228. He also drew attention (p.244) to comments in a recent letter to him from Lewis Mumford, who was aiming to establish the *Journal of Humanistic Psychology*: 'How nice, dear Julian, to find that such an early work of yours on the grebe gave ethology its start - and therefore the extension of pure ethology to cover human behaviour in all its

opinions were as strong as they were different from Zuckerman's: 'I strongly resent it ... when an American journal masquerades under the title of 'comparative' psychology, although, to the best of my knowledge, no really comparative paper has ever been published in it'. Gottlieb notes that Lorenz's definition of 'comparative' is based on the concept of homology - it is therefore exceedingly strict and few even ethological studies qualify for the adjective in the strict sense of the word.[115] However, Desmond Morris, at least, was a comparative worker, and he used this exciting and interesting theme to produce popular works which sharpened public attention on animal behaviour and its alleged significance in understanding human behaviour.

It has been suggested that Huxley's early development of sexual selection theory based on his study of bird courtship behaviour was meant to serve his wish to create analogies by which human social and political progress could be improved.[116] Furthermore, this would reflect the 'distinctively Edwardian genre of anthropomorphic animal biography'[117] as also produced by Selous and others at the time and which through popular science publications offered admiring accounts of the behaviour of a range of selected animals whose inferred 'morality', in terms for example of life-pairing, could be presented as worthy of emulation by humans.[118]

Huxley's support and influence therefore provided the main assistance for the establishment of ethology in Britain after the war,[119] together with the endeavours of

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aspects - intellectual, aesthetic, critical and religious - as well as the various displacement activities, physical and mental, that we practise when thwarted or checked in our aims'.

[115]Gottlieb, G. (1979) op. cit., p.164.

[116]Bartley, M.M. (1995) Courtship and continued progress: Julian Huxley's studies on bird behaviour. *Journal of the History of Biology*, 28: 91, 93 & 95.

[117]Durant, J.R. (1993) The tension at the heart of Huxley's evolutionary ethology. In: Van Helden, A. (ed.) (1993) *Julian Huxley: biologist and statesman of science*. Houston: Rice University Press, pp.253-255, cited by Bartley, M.M. (1995) ibid.

[118]See Peter Broks, 'Popular science and popular culture: family magazines in Britain 1890-1914', in *Three papers on the popularisation of science* (Lancaster: Centre for Science Studies and Science Policy, University of Lancaster, 1987), pp.4-28, cited in Durant, J.R. (1993) ibid. and Bartley, M.M. (1995) ibid.

[119]But in R.W.Burkhardt, Jr., 1992, 'Huxley and the rise of ethology' (in Waters, C.K. and Van Helden, A., 1992, ibid., pp.127-149), Huxley's role in founding the science of ethology is questioned, and it is proposed that rather than produce truly original work he presented in a format appropriate to the scientific community the work already completed by amateurs such as Selous and Howard, being more a synthesizer than an originator. M.M.Bartley (1995) (ibid., p.92) adds: 'Huxley was not the first to find grebes interesting: dedicated amateur birders such as Edmund Selous and W.P.Pycraft had written articles on the courtship behaviour of the great crested grebe beginning ten years prior to Huxley's first grebe observation' (Edmund Selous, 'An observational diary of the habits - mostly domestic - of the great crested grebe (*Podiceps cristatus*)', *Zoologist*, 5 (1901), 161-183, 339-350, 454-462; 6 (1902), 133-144; W.P.Pycraft, 'Habits of the great crested grebe', *Field*, 118 (1911), 823-824); and 'Burkhardt points out that Huxley may have owed more to amateurs than he was willing to admit in print (Burkhardt, R.W., 1992, ibid., pp.225-6). In several instances, it appears that

W.H.Thorpe and N.Tinbergen. In 1940, the latter had been in contact with Huxley and David Lack, asking Huxley for information on the Institute for the Study of Animal Behaviour and describing his own research and that of Konrad Lorenz. He hoped for collaboration after the war and explained to Lack: 'There are so few really serious students of animal behaviour and yet there is so much to do. When the war is over, it will be highly necessary to reconstruct international co-operation in our science as soon as possible and the first thing to do will be to organize a kind of symposium with Lorenz and some other Germans to discuss a broad long-range program.'[120] The survival of the Institute for the Study of Animal Behaviour was extremely important for the future of ethology in Britain,[121] since it was able to take over from a debilitated Germany and Holland the role of being a focus for the revival of ethology after the war. In this role it was guided by W.H.Thorpe, who became, as a Cambridge zoologist, its president in 1949, and who had introduced from the early 1940s the ideas of Konrad Lorenz into Britain, via the *Bulletin of Animal Behaviour*. As soon as the war closed, Thorpe visited Lorenz in Austria and, having nearly succeeded in securing him in an appointment in the United Kingdom, also developed contact with the Dutch ethologist, Niko Tinbergen.

As a child, Thorpe had suffered from ill-health and this resulted in an early development of interest in natural history as an alternative to communal and sporting activities. His mother was advised to encourage him to undertake an agricultural degree at Cambridge, where he soon turned to zoology and economic entomology, later achieving a post at the Farnham Royal Parasite Laboratory of the Imperial Institute of Entomology. His Cambridge mentor, J.Stanley Gardiner, Professor of Zoology, invited him in1932 to become Lecturer in Entomology, whereupon he was able to consolidate his studies of the physiology and behaviour of insect parasites, and the orientation and 'pre-imaginal conditioning' of insects. His long-standing interest in birds continued, and his studies of olfactory conditioning in the 1930s focussed his interest on the relation between instinct and learning, and extensive reviews of animal learning resulted, on insects in 1943 and on birds in 1951.[122] He wrote: 'I think at quite an early age my religious feelings and my love of nature became welded together,

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he reinterpreted his own observations to coincide with some of Selous's observations'.

[120]Tinbergen, N. (1940a) Correspondence with Huxley, J., 17 February. In: *The Julian Huxley Papers*, Rice University, Houston, Texas, series III, box 14. (1940b) Correspondence with Lack, D., 26 February. In: *The David Lack Papers*. Edward Grey Institute, Oxford, item 155. Cited by Durant, J.R. in *Animal Behaviour* (1986) 34: 1601-16.

[121]Durant, J.R. (1986a) From amateur naturalist to professional scientist. *New Scientist*, 24 July, pp.41-4.

[122]Hinde, R.A. (1987) William Homan Thorpe 1 April 1902 - 7 April 1986. *Biographical Memoirs of Fellows of the Royal Society of London*, 33: 621-39.

and - quite naturally and subconsciously of course - the world of living things came by way of a kind of nature mysticism to have what I should now call a primarily sacramental quality'. His close associate Hinde believed that 'his studies of animal behaviour were guided by the view that some element of self-consciousness could be traced in the animal kingdom, and he therefore laid himself open to the charge of preferring complex to simple explanations, though more recently the climate of opinion has moved more in his direction'.[123] Much like Julian Huxley and to a lesser extent like E.S.Russell, he believed that ethology and comparative psychology could help man understand his own nature, circumstances and prospects. His concern for the role of general science was shown by his inauguration at Cambridge of a scientists' lunch club in the McCarthy era in the 1950s, through which, like Zuckerman's 'Tots and Quots', issues connected with the social responsibilities of science and scientists could be discussed.[124]

The arrival of ethology resulted in experiments of a wider variety conducted in a greater number of species in more depth by a larger number of scientists possessing a mixture of backgrounds, as often reflected by their place of work.[125] Not all the researchers were connected with Thorpe or Tinbergen, as was Desmond Morris, who in 1958 tested the drawing abilities of Congo, a chimpanzee in the London Zoo, and demonstrated that chimpanzees show the basic elements of composition and patterning in their 'art'.[126] In the mid-1950s, Michael Chance, a zoologist, had begun a new wave of research on the rhesus monkeys at the London Zoo.[127] He attempted to improve on the assessment of the nature of their social structure, following the incorrect conclusions that Zuckerman had drawn owing to the effects of overcrowding of the animals at the time of his studies in the 1930s. Professor David Katz came to Britain as a refugee from Germany, and the Institute for the Study of Animal Behaviour helped him to undertake research, along the lines of its aims to assist behavioural research projects. Soon he was supervising the work of Åse Grude Skard, who came from Oslo, concerning the social behaviour of domestic fowl.[128]

Ethology set out to tackle some of the problems of experimental study which laboratory psychologists in Britain found particularly difficult. These problems centred

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[123] Ibid., p.631.
[124] Ibid., pp.630-3.
[125] See Appendix I.
[126] Morris, D. (1958) *The story of Congo*. London: Batsford.
[127] Chance, M.R.A. (1956b) Social structure of a colony of Macaca mulatta. *British Journal of Animal Behaviour*, 4: 1-13.
[128] Pear, T.H. (1955) The Manchester University Department of Psychology, (a) 1909-1951. *Bulletin of the British Psychological Society*, 26: 21-30.

on the identification and control during experiment of the internal factors affecting the behaviour of an organism. For the laboratory psychologists the independence from quantification of these internal factors posed a severe threat to scientific objectivity. American behaviourists had tried to overcome the difficulty simply by denying their existence and by concentrating on external evidence alone. The ethologists found that their research could proceed quite properly if the internal factors were described if not explained as components of an 'innate releasing mechanism'. For the British experimental psychologists, who in the main refused to adopt the Americans' behaviourist solution, the tendency arose to postpone the time for proposing theories, and to place hope in future biological and physiological discovery instead. There was also some fruitful interaction with the ethologists. O.L.Zangwill expressed his optimism in 1950: 'It is my belief that the foundations of an empirical psychology have been securely laid during the past sixty years ... a central biological science of psychology is in process of formation ...[but]... it is urged that the elucidation of central nervous mechanisms in relation to behaviour is a central problem in modern psychological research.'[129] Of course introspection could not be considered as a source of explanation, and so while faith was put in hoped-for physiological discoveries, theory-making was delayed and research became empirical. The reliance on physiology has continued, and has been seen by some as a threat to the viable independence of psychology.[130]

After a visit to America, Bartlett appeared to hint at the adoption of some of the methods accepted there as a way forward (but not necessarily with his approval): 'All animal behaviour is seen both as specifically directed, and as readily and widely adaptable ... It may be - I think it will be - that this twist towards the experimental study of skilled sequences in performance, will turn out to be by far the most lasting and radical movement in present-day psychology.'[131] Looking back in 1969, Hearnshaw criticized the practice that had grown of conducting experiments without clear theoretical frameworks:

> British psychologists in general have been prepared to borrow from various sources, and have been eclectic even to the extent of tolerating contradictions and ambiguities. The demand for clarity, for system, for theoretical neatness has seemed to them premature. Theory and empirical enquiry must rather go hand in hand, and the one cannot

[129]Zangwill, O.L. (1950) *An introduction to modern psychology*. London: Methuen, preface & p.20; c.f. Craik, K.J.W. (1945) The present position of psychological research in Britain. *British Medical Bulletin*, 3: 24-6.
[130]Joynson, R.B. (1970) op. cit.
[131]Bartlett, F.C. (1955) Fifty years of psychology. *Occupational Psychology*, 29, 4: 203-16.

> advance far beyond the other. The emphasis has been on method, rather than on theory, on experimental method by the Cambridge psychologists ... There has been an almost naive faith that something, some limited gains, will emerge from experimental or statistical data honestly and carefully collected. The need for theoretical guidance has often hardly been recognized ... Today the influence of McDougall has almost, if not completely, disappeared. Much more influential is the essentially empirical, anti-theoretical, Cambridge school under its successive directors, C.S.Myers, F.C.Bartlett, and O.L.Zangwill - experimental, but not methodologically doctrinaire, concerned with investigating manageable problems and keeping close to the complexities of human behaviour as found in real life situations, occupational, clinical and social ... British psychologists have for the most part been content to leave theory to the philosophers.[132]

Therefore, although Bartlett had criticized American scientists for too much procedure at the expense of theory, ironically Hearnshaw echoes Bartlett's criticism of them in himself criticizing the results of American influence soon after on British psychologists, including Bartlett. Bartlett's transmission of this influence on studies of animal behaviour was, however, indirect. Writing of him the year after his death in 1969, Broadbent commented:

> In the interval of nearly twenty years since Bartlett's retirement from his chair [in 1952] there have been enormous changes in British psychology ... his thinking drew little from an evolutionary source, and placed no emphasis on the structure of the brain. Nowadays these missing areas have been rightly and eagerly developed, and British psychology is heavily weighted towards rats, monkeys, brain lesions and effects of stimulating parts of the nervous system. This is in no way to be regretted, and only repeats on the national scale the early alliance of psychology and physiology in Cambridge. But its debt to Bartlett is indirect, and only through his training of psychologists who saw the importance of these areas for themselves.[133]

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[132]Hearnshaw, L.S. (1969) op. cit., pp.6 & 7.
[133]Broadbent, D.E. (1970) Frederic Charles Bartlett 1886-1969. *Biographical Memoirs of Fellows of the Royal Society of London*. Vol.16, p.8.

CHAPTER 5

POST-WAR PROFESSIONALIZATION

Introduction

Between 1940 and 1960 British psychology became less insular. Ethological methods were imported and flourished, and in the laboratory greater use was also made of American methodological techniques for the study of learning, conditioning and the effects of drugs, lesions and extirpation on behaviour. Important developments in the 1940s and 1950s took place not only in the British Psychological Society but also in the new Institute for the Study of Animal Behaviour and the Experimental Psychology Group. There was also a considerable expansion of university facilities, and hospital research became more influential. Generally, animal behavioural studies began to fragment into diverse areas and to serve different interests and purposes, many now applied, and this development had consequences for professionalization and organization. For example, as a conscientious objector, Thorpe had applied entomology to the war effort towards self-sufficiency in food production, contributing to a project on wire worms, which were causing serious agricultural damage, and this developed his general investigations of insect behaviour.[1]

It was after the war that the effect of the 'reputational system' became more clear, contributing a structure for the organization and control of research in this as well as other scientific areas that involved comparative task uncertainty. A reputation would be created by convincing innovation which was of relevance to allied scientific research and to institutional and societal requirements. Reputations would then contribute to professionalism and professional identity, and to influence, recognition and approval, leading to better employment opportunities and research facilities, with the underlying support of more efficient communication through increased publication. A further effect of the system as it developed was competition, testing, refinement and further progress. The requirements of the system for scientific subject areas were more demanding than in other professions (because of the task uncertainty), but as a result the scientific community in a given specialist area has become stronger and in turn

[1]Hinde, R.A. (1987) William Homan Thorpe 1 April 1902 - 7 April 1986. *Biographical Memoirs of Fellows of the Royal Society of London*, 33: 621-39.

strongly influences what emerges as scientific knowledge from among colleague competitors.[2]

In the sphere of animal behaviour studies, the reputational rivalry was soon seen in the broad disagreements between laboratory psychologists and ethologists. But beyond this simple division, many others reflected the wide ranging purposes and methods related to the subject. As professionalism and institutional organization grew, the whole field was therefore made up of a great variety of specialist activities, groups and individuals, as often competing as co-operating in what remained scientifically a comparatively new as well as uncertain subject area. Many of the components of this broad subject area had also remained of interest to those outside the immediate centres of research activity, and external influences on progress and direction were therefore strong.[3]

Studies of animal psychology and behaviour existed in a loosely structured field marked more by innovation and new avenues of interest than the cautious and conservative development of conventional, well-established theories. This meant that, though healthier and in greater evidence after the war, professionalization and institutionalization were fragmented processes and, as a result, comparatively restricted; and the effect of innovation has also at times brought into question the identity and relevance an entire subject within the field (that of comparative psychology, for example).

These largely internal sources of influence on the development of the general subject have to be set against the external political and administrative conditions evolving after the war. As one who had spent his life both as an academic and as a civil servant before and after the war, Sir Henry Tizard identified difficulties for science that seemed not to have changed. He spoke in 1955 of the 'deplorable intellectual gap that exists between those who have had a scientific education and those who have not. Practically all Ministers and members of the administrative civil service belong to the latter class'.[4] Zuckerman had been concerned that there had been no plans to use the

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[2]See Whitley, R. (1984) *The intellectual and social organization of the sciences*. Oxford: Clarendon Press, pp.11ff & 28.

[3]'Where ... researchers have a wide variety of legitimate audiences for their work, including educated laymen, and research skills are not highly standardized, as in many of the human sciences, the need to co-ordinate research results with those of a particular group of colleagues to gain positive reputations is limited, and so contributions to intellectual goals are relatively diffuse and divergent. Integration of task outcomes around common objectives is, therefore, not likely to be very high in such fields.' (Whitley, ibid., p.26).

[4]Tizard, H. (1955) *A scientist in and out of the Civil Service*. Haldane Memorial Lecture, Birkbeck

universities or scientists in preparation for the war, and had helped prepare in 1938 a memorandum on 'Science and National Defence' the gist of which was made publicly known in *Nature*. In 1945 he submitted to Herbert Morrison a further memorandum on the need for a central Government Science Secretariat.[5] However, very soon after the war the new Labour government had set up an Advisory Council on Scientific Policy,[6] and public expenditure on science began to escalate, soon buoyed partly by the effects of the Cold War and the accompanying research into weapons and space. From the late1940s there began a marked and then a steady rise in the production of science graduates, although the biological sciences tended to lag behind mathematics, chemistry and physics.[7] In 1959 the Conservatives on entering office appointed a Science Minister. By that time government expenditure on civil research, largely through the Research Councils, had increased from £4 million in 1945-6 to £29 million, although expenditure per head on research and development was in real terms less than 75% of that in the United States and the need for a better public appreciation of science was still thought necessary.[8]

Soon after the war's end, the opportunity was taken to examine the value of studies in animal behaviour in war and peace,[9] and of the analogy between the adaptations of animals in their natural environment and the inventions of man:

> Almost every invention ... has its counterpart in the modifications and behaviour of various wild creatures. To realize the truth of this we have only to think of the use, by squids, of jet propulsion and smoke-screens; of poison gas by skunks and many insects; of chemical warfare by various termites ...; of armour, by tortoises and armadillos; and of the recently discovered system of echo-location in bats ...[and]... the use of those devices [colour resemblance, obliterative shading, disruptive

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College, University of London, 9 March.

[5] He warned: 'To revert to the pre-war position would be disastrous. Already Industries, Universities and Government Departments are bidding against each other for our very limited supply of good scientists'. Zuckerman, S. (1978) *From apes to warlords: an autobiography 1904-46*. London: Hamish Hamilton, pp.425-6.

[6] This resulted from the Barlow Report of 1946, to which Solly Zuckerman was a contributor, and which attempted to predict scientific university, educational and manpower needs, and then (successfully, in Zuckerman's later opinion) to ensure an appropriate government response. It was until 1965 the main civil scientific advisory body in British government, having replaced the earlier Scientific Advisory Committee. Gummett, P.J. and Price, G.L. (1977) An approach to the central planning of British science. *Minerva*, 15: 119-43.

[7] Argles, M. (1964) *South Kensington to Robbins: an account of English technical and scientific education since 1851*. London: Longmans, pp.100, 102 & 118.

[8] Ibid., p.132.

[9] Hindle, E. (1947) Zoologists in war and peace. *The Advancement of Science*, IV, 15: 179-86.

coloration and shadow elimination] which serve for concealment, for disguise, or for bluff.[10]

Means for the exploitation and protection from pests of food resources, and the recognition of the use to which, for example, principles of camouflage as applied in nature could be put in wartime, were able to be taken much more seriously in the Second World War than at the time of the First: the solutions provided by behavioural research were at last given credence, established and acted on with thoroughness. Subsequently, for example, Solly Zuckerman was asked from 1948 to 1956 to study the capacity of dogs to be trained reliably to detect buried explosives in non-metallic casings, as they did buried bones.[11] At the conclusion of the European war Bartlett at Cambridge realized the expansion and recognition of his subject resulting from its military applications, and envisaged an early demand for more university - trained psychologists, necessitating an enlargement of his department at least. The immediate extra teaching load itself deserved the appointment of two demonstrators in experimental psychology.[12]

Generally in science, from the First World War 'emerged the germ of national science planning. The second gave tangible form to the governmental interventionism which has subsequently come to play such a noticeable part in the science policy of Britain and other countries'.[13] While the First World War resulted in a public loss of faith in the main constituent parts of the establishment, science survived this disillusionment as symbolic of success and a new future, and its popular esteem strengthened in the inter-war years. At the end of the Second World War, it was commonly accepted that scientists should help secure the post-war economy, and no serious public suspicion of science appeared until the organized protests against the bomb in the late 1950s and the general questioning of establishment values that developed in the 1960s.[14] Since

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[10]Cott, H.B. (1948) Camouflage. *The Advancement of Science*, IV, 16: 300-9.

[11]This resulted in the examination of 'mine-dogs' and 'tracker-dogs' and the findings remained of relevance in the 1980s in the aftermath of the Falklands War. Using the principle of conditioned response in their training of dogs, Zuckerman, together with J.T.Eayrs and Eric Ashton, studied the process by which dogs discriminated between different smells and reacted to disturbed ground. Zuckerman, S. (1988) *Monkeys, men and missiles. An autobiography 1946-1988.* London: Collins, pp.150-3.

[12]Cambridge Univ Lib MS Room. Add. MS. 8076. D.2.4, undated, c1945. In reference to Frederic Bartlett, Broadbent said that the sudden blossoming of new technology in the Second World War raised many questions requiring a psychological answer which he tried to find, and the Cambridge laboratory became a centre for many investigators of different backgrounds and purposes, some psychologists, some from medicine, some from the Services. Broadbent, D.E. (1970) Frederic Charles Bartlett 1886-1969. *Biographical Memoirs of Fellows of the Royal Society*, vol.16, p.5.

[13]Poole, J.B. and Andrews, K. (eds) (1972) *The government of science in Britain.* London: Weidenfeld and Nicolson, pp.2-3.

[14]c.f. Jenkins, E.W. (1979) Sources for the history of science education. *Studies in Science*

then science has occupied a paradoxical position both as the object of criticism, often from liberal and 'environmental' sources concerned with a variety of ethical issues, and as the source itself for the public of fascinating discovery and media-friendly speculation. For laboratory-based animal behaviour studies, a great deal of negative public attention has been brought to bear since the mid-1970s, resulting from the perception of a non-medical science dependent supposedly on sinister (rather than simply painful) experimental procedures often serving seemingly trivial or questionable ends.

The economic advantages to be gained after the war from behavioural studies were nevertheless better recognized, as shown, for example, by the post in animal behaviour at the Agricultural Research Council Poultry Research Centre in Edinburgh, advertized in the *Bulletin of Animal Behaviour* (No.6) in January 1948 and intended to serve the poultry industry. Meanwhile, efforts were being made to encourage the veterinary profession to take up behaviour studies: J.T.Edwards, by the time of his death in 1952 was said to have done more than anyone to bring veterinarians and animal behaviourists together.[15] Thorpe[16] laid great emphasis on the opportunities for workers in veterinary science and animal husbandry to employ animal behaviour studies not just for industrial and economic reasons but also for pure science itself. Workers in applied fields often conveniently had numerous, easily kept, controlled and bred experimental material. Co-operation could enable new advances in the understanding of, for example, the changes in instinctive behaviour which took place with domestication, and both pure and applied science would then benefit.

Behavioural experimentation took on a new purpose when it was used to assist in the development of clinical psychology, introduced to Britain after the war and vigorously promoted by H.J.Eysenck (d.1997). This resulted in a further field where it was thought advantageous to apply researches into animal behaviour. One who believed in this most strongly was the 'applied experimental, objective scientist' type clinical psychologist, Eysenck, of the Maudsley Hospital (Institute of Psychiatry).[17] He believed that both animals and men possessed introvert/extrovert and stable/neurotic personalities; that these varied according to the individual subject and could be measured; and that because animals, for example, rats, could be bred to express a

Education, 6: 52.
[15]Worden, A.N. and Cross, B.A. (1953b) Editorial: Grazing behaviour. *British Journal of Animal Behaviour*, I, 4: 123.
[16]Thorpe, W.H. (1953) Editorial. *British Journal of Animal Behaviour*, I, 1: 3-4.
[17]Gwynne Jones, H. (1969) Clinical psychology. *Supplement to the Bulletin of the British Psychological Society*, 22: 21-3.

particular level of emotionality and conditioned to behave in a desired manner, they should be experimented on as an aid to clinical psychology. Eysenck employed learning theory and behaviour therapy to tackle the problem of the neuroses, and drew inspiration both from Watson and Wolpe. In 1948, the Maudsley had amalgamated with the Bethlem Royal Hospital, and soon after, benefiting from an award under the Fulbright scheme, the American psychologist Roger Russell set up the animal laboratory at the Bethlem which was to play a special part in Eysenck's plans. For a time, Russell supervised the animal research after he had replaced Burt in the chair at University College in 1950. P.L.Broadhurst, who had studied animal psychology at Stanford University in California (to which he later returned for a year's fellowship at the Center for Advanced Study in the Behavioral Sciences) and who became director of the animal psychology laboratory at the Institute of Psychiatry greatly developed the animal laboratory when it fell to his charge between 1951 and 1963.[18] Work on genetics was carried out and rats were selectively bred for psychological characteristics.[19] Mice as well as men could show the effects of personality: Eysenck referred to a study in which the effects of alcohol fumes on six different strains of mice were studied. Two strains improved their performance; two strains declined; and two strains behaved just the same.[20]

The period between 1940 and 1960 saw an expansion of university honours courses in psychology, the establishment of research units, and the organization of professional psychology (clinical, educational, etc.), with a resulting increase in job opportunities. Hearnshaw points out that prior to 1960 the growth of student numbers in psychology was fairly closely tied to demand and job opportunities: if anything, in the period between 1940 and 1960, supply lagged behind demand. 'In 1960 there were 199 honours graduates completing their first degrees in psychology at British universities; by 1967 the number had risen to 667.'[21] This large increase meant that supply had overtaken demand, and a 'brain drain' took place, especially to America, where the English language and better facilities were available.[22] In 1964, while this was happening, Hearnshaw wrote: 'Today the young British student of psychology is brought up largely on American textbooks, and his gods, if he has any, are probably

[18]He claimed: 'There is essentially only one basic scientific interest in the study of animal behaviour and that is to learn more about man himself. The pursuit of knowledge for its own sake is often spoken of but rarely practised in pure form.' Broadhurst, P.L. (1963) *The science of animal behaviour*. Harmondsworth, Middlesex: Penguin Books Ltd, pp.13-14.
[19]Gibson, H.B. (1981) *Hans Eysenck: the man and his work*. London: Peter Owen, pp.83 & 94.
[20]Cohen, D. (1977) *Psychologists on psychology*. London: Routledge & Kegan Paul, p.102.
[21]Hearnshaw, L.S. (1969) Psychology in Great Britain: an introductory historical essay. *Supplement to the Bulletin of the British Psychological Society*, 22: 5-7.
[22]Hearnshaw, L.S. (1969) ibid., p.9.

American. 1940 was in more ways than one the end of an epoch.'[23] After the close of the Second World War, Craik[24] had considered the direction future work might take and hoped there would be more fundamental research on the special senses and on muscular movement. Electronic advances made in previous years should increase the scope of nerve and muscle action-potential recording, and so permit closer correlation between psychological experiments on sensation and physiological experiments on the sensory pathways. This correlation could also be used to examine homeostatic self-regulating systems in the body, analogous to the recently developed servomechanisms of the engineer.

New societies and journals

The Institute and Association for the Study of Animal Behaviour

The reasons for the foundation of the Institute for the Study of Animal Behaviour have already been mentioned briefly, and included a desire for emphasis on co-operation, communication and research by a variety of specialists. Inevitably, this led to a valuable stream of publication throughout the period. After its foundation in 1936 and until 1952, the Institute published at irregular intervals the *Bulletin of Animal Behaviour*. The first issue appeared in October 1938 with the object of providing a review of recent studies in animal behaviour. Intended as a quarterly, the next issue appeared only in May 1939, and then the outbreak of war led the Institute to suspend publication. However, the editors (J.W.B.Douglas and S.Zuckerman of the Department of Human Anatomy, Oxford) announced in the third issue of October 1941 that the decision of the Council of the Institute on suspension of publication had been reversed, because contributions had continued to come in. It was intended to continue the original policy of publishing mainly reviews, but from now on original contributions would be favourably considered.

In 1949 the Institute changed its name to the Association for the Study of Animal Behaviour. From 1948 its members had contributed to the international journal *Behaviour*, but they soon decided to publish their own journal. Consequently in 1953 the Association began the publication of the quarterly *British Journal of Animal*

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[23]Hearnshaw, L.S. (1964) *A short history of British psychology 1840-1940*. London: Methuen, pp.vi-vii.

[24]Craik, K.J.W. (1945) The present position of psychological research in Britain. *British Medical Bulletin*, 3: 24-6.

Behaviour, containing original scientific papers and reviews. By 1954 the Association had a membership of about 250, and held meetings at least four times a year. Many members were foreign, especially American, and because of the number of international contributors to the Journal, it was renamed *Animal Behaviour* in 1958, but continued from the previous volume's sequential number. By this time, too, the new Section of Animal Behavior and Sociobiology of the Ecological Society of America had become linked, after negotiations, with the Association. The Association maintained a library and membership was open to 'all who have a genuine interest in animal behaviour', including veterinary practitioners and farmers.

The nature of the work of interest to the Association was described by the Hon. Assistant Secretary, B.M.Foss, in 1954. Meetings of the Association of interest to psychologists could be illustrated by a symposium on rat behaviour held at Birkbeck College on 9 and 10 July 1953, when papers were read by ecologists, endocrinologists and psychologists. The scope of the symposium was indicated by some of the titles: 'Hormones and central maturation'; 'Selection of food by wild and laboratory rats'; 'The visual world of the rat', etc. Foss noted that the audience consisted of members from many different fields of study, so there was considerable cross-fertilization of ideas, this being one of the main practical functions of the Association. The discussions were introduced by Professor R.W.Russell and Professor W.Verplanck, both of whom interpreted the substance of the non-psychological papers in psychological language. These discussions centred on problems such as the relevance or irrelevance of ethology to learning theory; concepts of abnormality as applied to animals; the value to be attached to physiological interpretations of behaviour at the current stage of behaviour theory; as well as problems of a more factual nature.[25] When *Animal Behaviour* was published in 1958, it emerged as a much larger journal with the addition of American scientists to the editorial board.[26] The exchange of ideas and international communication therefore improved as the journal's circulation increased, and each method of investigating animal behaviour borrowed, lent and adjusted.

The history of the Institute and Association has been fully described by J.R.Durant, and much of the historical analysis of the organization which appears below reflects his original interpretation.[27] The Institute originally aimed to provide incomes for research

[25]Foss, B.M. (1954) Association for the Study of Animal Behaviour. *Bulletin of the British Psychological Society*, 22: 16-17.
[26]Worden, A.N. (1958) Editorial. *Animal Behaviour*, VI, 1-2: 1-2.
[27]Durant, J.R. (1986b) The making of ethology: the Association for the Study of Animal Behaviour, 1936 to 1986. *Animal Behaviour*, 34: 1601-16. In this article a thorough assessment is made of the academic, political and international contexts in which the organization developed, as well as of the

workers and to provide grants for special work or for the purchase of apparatus; and also to provide and maintain laboratories and field stations at which research could be carried out both in the laboratory and under natural conditions. But Durant points out that after 1939 the Institute funded no significant research at all; from its original aim of founding a discipline, it had been reduced to little more than a holding operation until the war was over, but in the meantime it did manage to continue with a small-scale programme of occasional meetings. Many Council and Annual General Meetings were held by post, but the Institute collaborated again with, for example, the British Psychological Society in the organization of a joint meeting in the summer of 1941. A meeting with the Royal Society of Medicine on the general theme 'The limitation and uses of the comparative method in medicine: comparative psychology and animal behaviour', on 21 June 1944 in London, included papers by C.S.Myers (Instinct), W.H.Thorpe (Learning processes in animals), D.B.Johnstone-Wallace (Grazing habits of beef cattle), and A.Walton (Comparative sexual behaviour in the male).[28] Another meeting on 25 October of the same year with the British Society of Animal Production and supported by the newly formed Committee on Animal Nutrition of the Agricultural Research Council examined grazing behaviour in sheep and cattle. In this area, 'the study of animal behaviour would be expected to have a great influence in making a science of what is now known as the stockman's art.'[29] Durant notes that:

> The fact that this was possible at all reflected in part the determination of the British government to maintain the academic life of the country through the war, and in part the zeal of just one or two Council members: Kirkman, who was the backbone of the Institute until shortly before his death in May 1945; Russell, who took over as President from Huxley in 1942; Thorpe, who was elected to membership in 1943 and rapidly assumed a position of intellectual leadership in the Institute; and Alastair Worden, who was elected to membership in 1941, became Secretary-Treasurer in 1945 following Kirkman's death, and thereafter played a central part in the running of the Institute for the next two decades.[30]

And in spite of wartime demands and distractions, the continuing, but intermittent publication of the *Bulletin* was tangible proof of the survival of the Institute during the war. After the close of hostilities, remarks Durant, Worden and Thorpe set the

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roles of key individuals.

[28] *Bulletin of Animal Behaviour*, vol.1, no.4, October 1944.

[29] J.Hammond, quoted in the editorial of the *British Journal of Animal Behaviour*, vol.1, no.4, 1953, p.123.

[30] Durant, J.R. (1986b) op. cit.

Institute on its feet. The former had conducted membership drives, so that numbers increased from 53 at the beginning of 1944 to about 150 by its end. Thorpe assumed an editorial interest not only in the *Bulletin* but also in Tinbergen's new journal, *Behaviour*, of which he was a founding editor and which enjoyed the support of the Institute. Furthermore, Thorpe set up in 1945 an Institute sub-committee to investigate the possibility of creating a research station. He was joined in this by James Gray,[31] the head of the Zoology Department at Cambridge, Edward Armstrong and David Lack, the newly appointed Director of the Edward Grey Institute of Field Ornithology in Oxford. After nearly five years of planning and negotiations, continues Durant, Thorpe steered through the establishment of an ornithological field station at Madingly near Cambridge, where the relationship between instinct and learning could be thoroughly investigated, making use of 60 aviaries. With Robert Hinde as its first curator, as well as Thorpe and a technician, this field station (which later became the University of Cambridge Field Station for the Study of Animal Behaviour and then the Sub-department of Animal Behaviour) represented the fulfilment of one of the Institute's central aims.[32] Soon G.V.T.Matthews joined to study bird navigation and Peter Marler to carry out field studies of the chaffinch.

Further scientific meetings of the Institute took place in 1946 and 1948, when the following papers were read (as recorded in the *Bulletin of Animal Behaviour*, January 1948): 'Observations on social behaviour induced in mice by sympathomimetric amines', by M.R.A.Chance (Glaxo Laboratories Ltd, Greenford, Middlesex); 'The keeping of hedgehogs under laboratory conditions and observations on their behaviour', by J.T.Edwards (Foot and Mouth Disease Research Station, Pirbright, Surrey); 'Some observations on the behaviour of pigs in an experimental piggery', by R.Braude (National Institute for Research in Dairying, University of Reading); 'Some observations upon behaviour in sheep with particular reference to grazing habits and to climate', by R.Phillips (Department of Animal Health, University College of Wales, Aberystwyth); 'Some new aspects of post-convulsive behaviour in Peromyscus', by M.R.A.Chance and D.C.Yaxley (Department of Pharmacology, University of Birmingham); 'Some psychological factors relating to convulsive behaviour in rats', by Professor G.Humphrey (Department of Psychology, Oxford University); and 'Canine hysteria', by Sir Edward Mellanby (Medical Research Council).

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[31] R.A.Hinde (1987, op. cit., p.627) recalls that Gray's enthusiasm waned, partly because of his antipathy to the Lorenzian views that Thorpe shared.
[32] Durant, J.R. (1986b) op. cit., p.1612.

Meanwhile David Lack was helping Tinbergen to establish contact with Oxford, and, impressed with the efforts of Thorpe and the Institute, he was persuaded to accept a lectureship in animal behaviour there. In this way it seems that the Institute played a small part in the establishment of the Animal Behaviour Research Group in Oxford. After 1950, Cambridge and Oxford became the twin foci of ethology in Britain. By then the Institute had become an Association, and the change was marked appropriately by the joint Institute for the Study of Animal Behaviour / Society for Experimental Biology Cambridge conference in July 1949 on 'Physiological Mechanisms in Animal Behaviour': the meeting was both the last major achievement of the Institute and the first formal activity of the renamed Association for the Study of Animal Behaviour; and in retrospect it therefore seems especially appropriate that one subject for a round-table discussion had particular significance for the process of professionalization in animal behaviour studies. This concerned an attempt to reach agreement on terms and nomenclature used in behavioural research between those who represented the various fields of animal behaviour study.[33] Thorpe also took the opportunity to express his views on the relationship between instinct and learning.

The creation of the Association indicated its shift away from the increasingly redundant aim of being a centre for ethological research and towards the increasingly necessary aim of being a specialist society for the promotion of an emerging scientific discipline; and with the introduction of its journal in 1953 it assumed the form it has since kept. This journal had been produced after considerable worries over membership levels and finance in the very early 1950s: it was Thorpe's idea, brought to reality by the work of the Treasurer, James Fisher, and it immediately strengthened the Association with academic recognition and subscriptions. Five years later its transformation into *Animal Behaviour* heralded a major move on the part of the Association towards international recognition, and further membership increases took place. Between 1953 and 1967, C.R.Ribbands held the post of Treasurer and his business sense helped further to make the finances of the Association secure, but without raising the membership subscription.[34] Durant concludes his history of this organization by observing:

> For the past 50 years, the Institute / Association for the Study of Animal Behaviour has grown along with the growth of ethology. Indeed, the two cannot strictly be separated; for to a large extent the growth of the Association (and of its sister organizations in other

[33]Thorpe, W.H. (1951) The definition of some terms used in animal behaviour studies. *Bulletin of Animal Behaviour*, 9: 34-40.
[34]Kalmus, H. (1967) Obituary: C.R.Ribbands. *Animal Behaviour*, 15, 4: 402 .

> countries) is the growth of ethology. The founders of the Institute looked forward to the unification of what Huxley, in a circular letter in March 1941, to a membership which was scattered and shattered by war, referred to as 'three sets of workers at present much divided from each other: the professional Zoologist, the Psychologist and the Field Naturalist. It is on their better understanding of each others' work and their closer co-operation', he wrote, 'that the progress of the Study of Animal Behaviour depends' (Association for the Study of Animal Behaviour Archive). The undoubted achievements of the Association for the Study of Animal Behaviour over the past half-century, and the prospects for still further achievements in the next, testify to the fulfilment of this, the founders' original and most far-sighted aim.[35]

After Tinbergen had accepted Sir Alister Hardy's invitation of 1949 to a post at Oxford and to develop an animal behaviour research group, he and Thorpe soon came to an informal agreement that the Cambridge group should concentrate on mechanisms and development of behaviour while the Oxford group should focus on behavioural functions and evolution. Accordingly, Tinbergen and his students undertook, for example, a major comparative study of the behaviour of gulls, while Thorpe and his colleagues investigated the development of song in birds. In 1950 Thorpe had moved to the four acre site at Madingley that the University had purchased for an ornithological field station. Lorenz had accepted an offer by Thorpe to superintend it, but then took up a more attractive proposition in Germany. Consequently, R.A.Hinde arrived as curator and began studies of species-specific behaviour in finches, imprinting in the moorhen, domestic chick and duck, and studies of song and song-learning, primarily with the chaffinch.[36] Thorpe himself had been attracted to the study of birds as suitable subjects because they provided 'on the one hand some of the most striking examples of elaborate instinctive behaviour (as in their display, feeding methods, nest building, etc.) and at the same time they were capable of extraordinary feats of learning (as in their migratory and homing orientation), and, in the song birds especially, of imitative learning of a high order. So I decided that at all costs I must attempt to switch over from entomology to ornithology.'[37] At Madingley, Thorpe found improved recording techniques and the invention of the sound spectrograph essential to his work. Without the sound spectrograph his work would have been very difficult, since he needed to tell at a glance the difference between the songs of birds

[35]Durant, J.R. (1986b) op. cit., p.1615.
[36]Asquith, P.J. (1981) *Some aspects of anthropomorphism in the terminology and philosophy underlying Western and Japanese studies of the social behaviour of non-human primates*. Oxford University: unpublished D.Phil. thesis, p.70.
[37]Thorpe, W.H. (1979) *The origins and rise of ethology: the science of the natural behaviour of animals*. London: Heinemann, pp.119-21.

with different experimental backgrounds.[38] Soon an aviary keeper joined the staff, and among the first students were G.V.T.Matthews (who made orientation studies in gulls, on the Manx shearwater, and on homing pigeons) and Peter Marler (who studied the aggressive displays of the chaffinch as examples of appetitive and consummatory behaviour, and from this developed his investigations into the song and the significance of its individual variation). In addition to these, Hinde carried out 'a critical study of the nature of the visual stimulus which the form and facial disc of owls present and which leads to the mobbing response of so many small birds. This included a detailed study of the birds' habituation to such models and the various circumstances which govern the rate and degree of decrement of the response over lengthy periods.'[39] At the same time, Thorpe was carrying out studies on imprinting and the following response of a number of species of precocial birds, and found that imprinting was not as irreversible as suggested by Lorenz's work: Patrick Bateson continued with this area of research when he later succeeded Thorpe. Another area of research involved a study of 'insight learning' in birds that were trained to pull up food with string, the learning process being closely analyzed in ensuing years by Margaret Vince. Further experimental work carried out at Madingley and then published is referred to below.

The Experimental Psychology Group and Society

'Sir Frederic Bartlett inculcated ineradicably in his students the principles of experimental methodology. The truth of the last point is reflected in the fact that all the founder-members of the Experimental Psychology Group [which became the Experimental Psychology Society] were ex-pupils of his.'[40] The Group was established in 1946 by a small number of young psychologists, nearly all of whom had been working in applied psychology during the war. Oxford, London, Edinburgh and Glasgow were represented, as well, of course, as Cambridge. The aim of the Group was to revive interest in basic psychological issues along experimental lines. A

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[38]Sparks, J. (1982) *The discovery of animal behaviour*. London: Collins, p.170. Thorpe would, for example, raise chaffinches in varying degrees of social isolation and then expose them to other chaffinches or tape-recorded songs to attempt to discover what was innate, and what was learned, and how. These enquiries led to much similar investigation, 'one of the most important enterprises in ethology,' and Peter Marler developed studies of song development in the United States; they also paved the way for detailed neurophysiological investigation of the mechanisms involved. Hinde, R.A. (1987) op. cit., p.628.
[39]Thorpe, W.H. (1979) op. cit., pp.122-3.
[40]Heim, A. (1971) Sir Frederic Bartlett. *Occupational Psychology*, 45, 1: 3-4. Broadbent (1970, op. cit., p.3) adds that the teaching system established by the 1930s 'produced a brilliant crop of students who, after the Second World War, held the lion's share of the Professorships of Psychology in Britain; and indeed quite a number elsewhere in the Commonwealth'.

benefaction from one of the members enabled the *Quarterly Journal of Experimental Psychology* to begin publication in 1948, the editorial board consisting of R.C.Oldfield (Editor), D.Russell Davis, G.C.Drew, G.C.Grindley, M.D.Vernon, T.W.Whitfield and O.L.Zangwill. General papers with an experimental bias were invited from, among other categories of scientists mentioned, 'the biologist at work upon perceptual functions in animals'. However, none of the forty-one articles of the first parts published up to the end of 1950 dealt with any aspect of animal behaviour. After then, the situation changed, and details of articles on animal behaviour are given below in the appendices. In the first quarterly edition, the rules of the Group were announced: membership was at first limited to thirty and was by invitation. The aims of the Group were meetings, publication and research, and not the furtherance of professional status for psychologists. In July 1949 a meeting was held in Cambridge in association with the symposium that had been organized jointly by the Institute for the Study of Animal Behaviour and the Society for Experimental Biology: Nancy Harris, P.H.R.James, C.Poulton and C.B.Gibbs gave, by invitation, short interim reports of work in progress at the Cambridge Psychological Laboratory.

O.L.Zangwill[41] stated that for most of its life the size of the Group was intentionally kept small to maintain internal cohesion and to allow for genuinely informal meetings and discussion. However, as the members grew older and new developments took place around them, it was decided to reconstitute the Group into a larger and more responsible Society. The new Society was launched in 1958 with 74 founder members. The rate of election of new members has nevertheless remained limited as a matter of policy and in order to ensure high scientific standards. Both the Group and the Society established the custom of electing to visiting membership experimental psychologists from abroad who came to work in Britain for periods of up to one year, and their influence was recognized as considerable. The interests of the Society have covered all branches of experimental psychology and related subjects, including ethology, neurophysiology and experimental psychiatry, and interdisciplinary work has been encouraged.

[41] Zangwill, O.L. (1969) The Experimental Psychology Society. *Supplement to the Bulletin of the British Psychological Society*, 22: 19-20.

The [incorporated] British Psychological Society

Having been founded at University College London in 1901,[42] the British Psychological Society was incorporated forty years later in 1941,[43] and by the institution of graduate associates and fellows a move was made to regulate the qualifications of its members. Many members assisted in the drawing up of the new constitution, especially Professor A.W.Wolters, President from 1938 to 1941. From 1958 onwards, further to protect the interests of both the public and trained psychologists, new members were required to possess qualifications equivalent to a first university degree in psychology. Others could subscribe and attend meetings but could not assist in the Society's government. In 1951 a category of student subscriber was created as an investment for later full membership.[44] Apart from the *Journal*, there appeared in 1948 a new quarterly *Bulletin*. Its purpose was to give news of the activities of the Society in all its sections and branches, and information about the work of psychologists in Britain and abroad. Correspondence would also be included. The editorial of the first issue commented:

> It has been suggested that ... unnecessary duplication of [research] work may be taking place. Publication here of the titles and authors of such enquiries, and notes on work in progress, may prevent that. It is also said that there is too little contact between psychologists working in different fields, that specialists in one branch of the subject are as ignorant as the general public of new developments outside their professional range of interest. Expository articles surveying conclusions reached in a specialized field over the last ten years are invited.[45]

In the post-war period the involvement of the Society in experimental work in animal behaviour, as reflected in the contents of its publications, was gradually reduced and replaced by that of the other recently formed specialist societies and journals. However, the Society has remained a strong voice for general issues in professional psychology, as when ethical questions concerning animal experimentation were raised in its *Bulletin* from the mid-1970s, resulting not long after in the establishment of a special working party, followed also by a new psychobiological section within the Society to represent experimenters' interests.

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[42] It then had 13 members, but nearly a hundred by the close of the First World War. In the 1980s its membership reached 10,000.
[43] Edgell, B., (1947) The British Psychological Society. *British Journal of Psychology*, XXXVII, 3: 113-32.
[44] Audley, R.J. (1969) The British Psychological Society. *Supplement to the Bulletin of the British Psychological Society*, 22: 16-19.
[45] Laws, F. (1948) Editorial. *Quarterly Bulletin of the British Psychological Society*, 1: 1.

Diversification and specialization in centres of research and teaching

Between 1940 and 1960 there was a significant increase in the centres of research undertaking psychological experimentation; this was represented by the expansion of existing departments and laboratories in universities, or their creation both in universities and in a few hospitals. Littman observes that for psychology it has only been since the Second World War that the earlier limitations of the university as a place for scientific research were overcome in England.[46] By 1939 there were seventeen British universities and the chairs of psychology in them amounted to six (at Manchester, Cambridge and Edinburgh, and in London at King's College, University College and Bedford College), with thirty lecturing staff. At the end of the war these numbers increased, so that by 1962 they were twenty and 200 correspondingly.[47] Hearnshaw comments that it was not until the 1960s that psychology became fully accepted into the academic curriculum, and found a place in most, but not quite all, British universities. Psychology still tended to be regarded as the province of philosophy. A short account of the state of animal psychology in British laboratories in the early 1950s is given by Drew and F.H.George (a lecturer in the Bristol Psychology Department of which Drew became professor in 1951).[48] In Cambridge psychology was taught as part of the Moral Sciences until 1951, although the growth of the Cambridge laboratory had made it an increasingly uneasy partner of logic and ethics. When Bartlett retired from Cambridge in 1952, a great era came to a close, for experimentation at the laboratory under his successor, Zangwill, increasingly took the form of both American physiological psychology and neuropsychology and the study of animal behaviour, as evidenced by ensuing publications such as *Cerebral*

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[46]Littman, R.A. (1979) Social and intellectual origins. In: Hearst, E. (ed.) (1979) *The first century of experimental psychology*. Hillsdale, New Jersey: Lawrence Erlbaum Associates, p.66.
[47]Hearnshaw, L.S. (1962) Sixty years of psychology. *Bulletin of the British Psychological Society*, 46: 2-10. Before the end of 1960, chairs of psychology existed at Aberdeen (established 1946, occupied by A.R.Knight 1947- 1963); Belfast (1958, G.Seth); Bristol (1951, G.C.Drew 1951-1958, K.R.Hall 1959-1965); Cambridge (1931, Sir F.C.Bartlett 1931-1952, O.L.Zangwill 1952); Durham (1952, F.V.Smith); Edinburgh (1931, J.Drever I 1931-1945, J.Drever II 1944-1966); Glasgow (1947, R.W.Pickford 1955); Leeds (G.P.Meredith 1949-1967); Leicester (1960, S.G.M.Lee); Liverpool (1947, L.S.Hearnshaw); Bedford College, London (1945, D.W.Harding); Birkbeck College, London, transferred from King's College (1944, C.A.Mace 1944-1961); London Institute of Education (1949, P.E.Vernon 1949-1965); Institute of Psychiatry, London (1955, H.J.Eysenck); University College, London (1928, C.E.Spearman 1928-1931, Sir C.L.Burt 1931-1950, R.W.Russell 1950-1957, G.C.Drew 1958); Manchester (1919, T.H.Pear 1919-1951, J.Cohen 1952); Nottingham (1960, W.J.H.Sprott); Oxford (1947, G.Humphrey 1947-1956, R.C.Oldfield 1956-1966); Reading (1943, A.W.P.Wolters 1943-1950, R.C.Oldfield 1950-1956, M.D.Vernon 1956-1967); and Sheffield (1960, H.Kay) (Kenna, 1969). At this time Hull also had a sizeable and vigorous department which was not headed by a professor: the non-professorial Head of Department was G.Westby.
[48]Drew, G.C. and George, F.H. (1953) Studies of animal learning. In. Mace, C.A. and Vernon, P.E. (eds) (1953) *Current trends in British psychology*. London: Methuen, pp.172-84.

dominance and its relation to psychological function (Zangwill, 1960) and *Current problems in animal behaviour* (Thorpe & Zangwill (eds), 1961).[49] Grindley, Drew and Thorpe were among a small number at Cambridge who had studied experimental animal behaviour in a systematic fashion in Bartlett's time. Some, like Kenneth Craik, had an interest in animal behaviour,[50] but were preoccupied with other matters. According to Margaret Vince,[51] who began working in the Cambridge Psychological Laboratory under Craik in 1943, there was no animal research undertaken between the time of her arrival and the advent to the chair of Zangwill: Craik undertook some animal work (none of it published) but in order to do this it was necessary to seek the (usually generous) co-operation of the Physiology Department.

In Oxford psychology was not taught at all as a degree subject, except as a minor adjunct of philosophy, until 1946.

> The philosophers reinforced prejudices. 'We possess already a wealth of information about minds' wrote Professor G.Ryle, the Oxford philosopher, in *Concept of mind* (1949). The job of the philosopher was merely 'to rectify the logical geography of the knowledge which we already possess', and as for psychology, as a unitary branch of science, it was nothing more than a dream resting on mistaken assumptions. Of course, not all philosophers have thought this way. But this kind of thinking was sufficiently widespread to make the task of establishing psychology in British universities, and of getting it accepted by educated opinion as a respectable branch of knowledge, an extremely slow and uphill task.[52]

A survey of all research published or abstracted between 1938 and 1959 in the five principal British journals and in *Behaviour* is given in Appendix I. The scope, nature and arrangement of this survey are described at its beginning, and as with subsequent surveys supplied in further appendices dealing with later periods (see below), it is possible to extract information linking research workers; work centres, cited as the source of papers; fields of interest (categorized as in *Animal Behaviour Abstracts*); experimental animals; publishing journal; and year of publication. It is also possible to identify joint authorships. The survey may be regarded as representative, although some relevant research was also published in journals which have not been used in this analysis because of the inconsistent or relatively infrequent presence in them of British

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[49]Sahakian, W.S. (1975) *History and systems of psychology*. New York: John Wiley & Sons, p.98.
[50]Sherwood, S.L. (ed.) (1966) *The nature of psychology: a selection of papers, essays and other writings by the late Kenneth J.W.Craik*. Cambridge: University Press.
[51]Vince, M.A. (1987) Personal communication, 25 March.
[52]Hearnshaw, L.S. (1969) op. cit., p.4.

behavioural work during the period in question. Such journals include, for example, *Advances in psychosomatic medicine*, *Behavioral science*, *Evolution*, *Ibis*, *Journal of agricultural science*, *Journal of comparative and physiological psychology*, *Journal of experimental biology*, *Journal of experimental psychology*, *Journal of physiology*, *Journal of psychosomatic research*, *Nature*, *Neuropsychopharmacology*, *Proceedings of the Royal Society (B)*, *Proceedings of the Zoological Society of London*, *Psychological Review*, and *Psychopharmacologia*. The full range of journals used to publish research on animal behaviour can be discovered in Category 4 of Appendix VII, containing data mainly from *Animal Behaviour Abstracts* and covering the later survey periods; but for this earlier phase an indication of the range is given, for example, by Broadhurst & Martin.[53] The comparative levels of frequency of publication of later British work in some of the journals mentioned above is identifiable in Category 4 of Appendix VII and may be regarded as a reflection also of the position before 1960. For example, clear frequency differences continue in the 1970s between journals such as *Animal Behaviour* or the *Quarterly Journal of Experimental Psychology* (high frequency), and American ones such as the *Journal of Experimental Psychology* or *Psychological Review* (very low frequency).

The survey shows that the *British Journal of Psychology* had continued to reduce its coverage of British animal behaviour work, and in later decades this coverage was all but relinquished (1940-1959: 11 articles; 1973-1980: 10 articles). Meanwhile, the ouput of *Behaviour* became steady throughout the 1950s (1948-1959: 71 articles), but because the *Quarterly Journal of Experimental Psychology* remained both in this period and later concerned to provide a coverage representative of all forms of experimental psychology, its treatment of British animal work was relatively limited (1949-1959: 26 articles; 1973-1980: 41 articles). The dominant position was eventually taken over by *Animal Behaviour*, having evolved from the *Bulletin of Animal Behaviour* which had managed to survive the war (1938-1951: 12 articles), and from its successor, the *British Journal of Animal Behaviour*, which itself achieved a very significant level of publication of British work in the mid 1950s (1953-1957: 95 articles). In its new role as an international forum for animal work, *Animal Behaviour* has subsequently remained the key journal for British research (1958-1959: 44 articles; 1973-1980: 171 articles). The general trend in British publication since the Second World War has shown a shift from the use of the traditional psychological journals to those with a greater orientation to zoology and ethology, together with the

[53]Broadhurst, P.L. and Martin, I. (1961a) Comparative and physiological psychology in Britain 1960. *Bulletin of the British Psychological Society*, 45: 41-55; and (1961b) The study of higher nervous activity in Britain. *Activitas Nervosa Superior*, 3: 164-76.

participation also of international journals representing applied psychological research, as in pharmacology (e.g. *Pharmacology, Biochemistry and Behavior*: 46 British contributions between 1974 and 1980).

During the post-war period ending in 1960 the journal survey, resulting in the identification of a total of 258 individual papers by 152 different authors, reveals a group of experimental scientists who were particularly productive in terms of their published output.[54] Five authors produced ten or more papers. Of these, Chance at the Department of Pharmacology in the University of Birmingham employed rodents to examine social behaviour and the effects of external and chemical stimulation and drugs. Free at the Bee Research Department of Rothamsted Experimental Station studied social spacing, maintenance behaviour and orientation. Hinde at Madingley investigated communication, social, sexual, reproductive and parental-filial behaviour and hormones in birds. Hurwitz of the Department of Psychology at Birkbeck College, London, examined conditioning, habituation, motivation and extinction in rats. Finally, the fifth of this group, Morris of the Department of Zoology and Comparative Anatomy at Oxford studied communication, sexual and reproductive behaviour, and evolution and survival value in fish and birds.

The data assembled for this period are also able to indicate by author attributions the dominant areas of interest of all those publishing their research activities in the representative journals chosen.[55] In the survey, 258 separate papers related to specific fields of interest have been identified. These involved 152 different authors, because of the occurrence of joint authoring. The activity of an individual in authoring a paper, singly or jointly, took place on 315 occasions. Of these occasions, 48 concerned publication on sexual and reproductive behaviour; 33 on maintenance behaviour (foraging, ingestion etc.); 27 on groups and social behaviour; and 21 on evolution and survival value. In the same way, it can be shown that mammals, excluding primates, and usually signifying the rat or mouse, have been the subjects of research on 132 of these occasions; insects on 78; and birds on 67. Other types of animal had very little use, and primates earned only three author attributions.[56]

The focus of research in animal behaviour was centred mainly on particular institutions associated with the published output, and the journal survey for this and later periods shows how as the extent of behavioural work increased, so too did the total number of

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[54]See Appendix I.
[55]See column c, Category 2 of Appendix VII.
[56]See column c, Category 3 of Appendix VII.

sites active in it.[57] Before 1960, using the same system of author attributions described above, among 81 productive sites, the most active were Madingley (36 out of the 315 attributions), the Department of Zoology and Comparative Anatomy at Oxford (25), Rothamsted (22), the Institute and Department of Experimental Psychology at Oxford (17) and Birkbeck (13).

P.L.Broadhurst and Irene Martin[58] carried out a survey by questionnaire of all departments engaged in studies of comparative psychology and animal behaviour in 1960, and the information they received is incorporated with the following account of some developments in such departments between 1940 and 1960.

At Aberdeen in 1948 in the Faculty of Arts and in 1953 in the Faculty of Science, it became possible to read for an honours degree in psychology alone, and there were also increases in staff serving the subject. In 1944 the Anderson Lectureship in Comparative Psychology was converted into a readership and in 1947 the readership became the Anderson Chair (of Psychology without any adjective - the 'comparative' element of the title as for the lectureship had been dropped some years before). By 1962 there were ten staff: A.E.Bursill, E.D.Fraser, M.K.Knight, R.Mitchell, J.S.Pollard, R.L.Reid, J.W.Shepherd, J.R.Symons, T.D.Taylor and Professor R.Knight, together with three technicians. Others who were members of staff since 1947 were Associate-Professor D.E.Berlyne, D.G.Boyle, J.W.King, A.J.Laird, M.F.McHugh, P.McKellar, B.Mandell, L.Simpson and F.V.Smith. Also by 1962 there were 302 students in the department, and a further increase of staff was urgently required, as was better accommodation. In 1948, the department had moved from the rooms and laboratory in Marischal College that it had occupied since 1906, and in 1962 it was spread over four different buildings in Old Aberdeen. A new department with thirty-six rooms and appropriate equipment was planned for 1963 or 1964. On the teaching side, the major development after the war had been the introduction of the full honours curriculum in psychology. Animal learning had been the subject of experiments (and of an article in *Nature*) as far back as 1932, and during the years leading up to 1962 was one of the principal interests of Berlyne and Reid, who both published numerous articles on the subject.[59] By 1960 the department was maintaining a colony of pigeons and had access to one of rats. Research on determinants of exploratory behaviour in the rat[60] was succeeded by work on operant conditioning,

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[57]See Category 1 of Appendix VII.
[58](1961a) op. cit.
[59]Knight, A.R. (1962) The Department of Psychology in the University of Aberdeen. *Bulletin of the British Psychological Society*, 47: 3-11.
[60]Berlyne, D.E. and Slater, J. (1957) Perceptual curiosity, exploratory behaviour, and maze learning.

especially in relation to extinction,[61] and in 1960 the laboratory programme also included a study of maze learning in earthworms.

In 1951 the University of Bristol Department of Psychology separated from Philosophy as an independent department, and K.R.L.Hall accepted a position as part-time lecturer, while continuing his work at Bristol Mental Hospitals. Psychiatrists and endocrinologists at the hospitals and members of the Psychology Department became involved in his research, lending him equipment and putting technicians at his disposal. At the hospitals he created a flourishing experimental unit with good facilities, but his interest in animal behaviour, especially that of birds and primates, did not result in active research until he left for Cape Town to become Professor of Psychology between 1955 and 1959. Soon after occupying the chair of psychology at Bristol on his return in 1959, and in succession to G.C.Drew, he managed to obtain vastly improved accommodation for the department.[62] As part of the programme of work in zoology, the habituation of Nereid worms to various stimuli was investigated,[63] and studies were made on aspects of the behaviour of bees.[64]

O.L.Zangwill[65] reported that at Cambridge in 1956 a new scheme was worked out designed to improve accommodation for the Departments of Physiology and Experimental Psychology. It envisaged a radical reconstruction of about three-quarters of the old psychology building to meet the pressing needs of the Department of Physiology while providing psychology with a new building which should incorporate a small part of the old laboratory, including the workshop. After various modifications this scheme secured the university's approval. Work on the new building began in May 1958; the Department moved to its new home early in 1960, and completion of the entire project was achieved late in 1961. The new laboratory was on four floors and comprised in all 20,500 sq. ft. In planning it the policy was, first, to expand teaching accommodation (which had remained unchanged since 1913); secondly, to provide adequate space and facilities for contemporary research interests, including work on

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Journal of Comparative and Physiological Psychology, 50: 228-32.

[61]Reid, R.L. (1958) Discrimination-reversal learning in pigeons. *Journal of Comparative and Physiological Psychology*, 51: 716-20.

[62]Drew, G.C. (1966) Obituary: K.R.L.Hall. *Bulletin of the British Psychological Society*, 19, 62: 43-4.

[63]Clark, R.B. (1960) Habituation of the polychaete Nereis to sudden stimuli: 2. Biological significance of habituation. *Animal Behaviour*, 8: 92-103.

[64]Free, J.B. (1958) The ability of worker honey bees (Apis Mellifern) to learn a change in the location of their hives. *Animal Behaviour*, 6: 219-23; Allen, M.D. (1959) The 'shaking' of worker honey bees by other workers. *Animal Behaviour*, 7: 233-40.

[65]Zangwill, O.L. (1962) The Cambridge Psychological Laboratory. *Bulletin of the British Psychological Society*, 48: 22-4.

animal behaviour; and thirdly, to achieve as much flexibility in the design of research accommodation as was consistent with foreseeable needs. Limitation of space made it impossible to provide accommodation for both teaching and research on a scale truly adequate, but experimental psychology was through these developments vastly better housed in Cambridge, and offered good facilities for research in a variety of fields of contemporary interest. The animal section occupied 2,470 sq. ft. on the second floor, was self-contained and fitted with an independent heating and ventilation system. Accommodation was available for up to sixty rhesus monkeys and 200 rats or other small mammals. The section contained two animal-keeping rooms, operating theatre and preparation room, post-mortem room, dark room and four testing rooms. On the same floor, though outside the animal section proper, were two communicating and partially sound-proofed rooms designed for work on birds, a room for histology, two offices and one large room for research students. Zangwill pointed out that experimental psychology in Cambridge owed much to the Professor of Physiology, Sir Bryan Matthews, who generously linked the needs of the Psychology Department with those of his own. H.T.Richardson was responsible for the first outline sketches of the new building, and G.C.Grindley, A.J.Watson and R.E.Stonebridge assisted with the solution of practical problems. Experimental work in Cambridge at the time centred on problems relating to brain physiology and behaviour with special reference to the effects of lesions and drugs.[66] Birds were used for the study of visual discrimination,[67] and in the Physiology Department the taste preferences of pigeons were investigated.[68] In the late 1950s and 1960s Zangwill and Thorpe organized a discussion group for psychologists and biologists to examine problems of behaviour.

Meanwhile, notes Durant, Thorpe's growing influence after the war was enough to ensure that the Institute for the Study of Animal Behaviour would remain faithful to the essentially ethological vision of its founders. Using the Institute, Thorpe promoted ethology through its *Bulletin*; organized translations of important work; explained Lorenzian instinct theory, and incorporated new ideas into research. He forged links with Tinbergen, Von Frisch and continental ethologists; arranged visits to and from the Netherlands and Germany; set up with Tinbergen the crucial joint Institute for the

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[66]Weiskrantz, L. (1960) Effects of medial temporal lesions on taste preference in the monkey. *Nature*, 187: 879-80; Gross, C.G., Oxbury, J.M. and Weiskrantz, L. (1959) The effect of meprobamate on auditory discrimination, delayed response and time interval estimation in rhesus monkeys. In: Bradley, P.B., Deniker, P. and Radouco-Thomas, C. (eds) (1959) *Neuro-psychopharmacology*. Amsterdam: Elsevier.
[67]Vince, M.A. (1959) Effects of age and experience on the establishment of internal inhibition in finches. *British Journal of Psychology*, 50: 136-44.
[68]Duncan, C.J. (1960) Preference tests and the sense of tasts in the feral pigeon (Columba livia Var. Gmelin). *Animal Behaviour*, 8: 54-60.

Study of Animal Behaviour / Society for Experimental Biology conference in Cambridge in 1949; and kept alive the struggle for the research station that later materialized at Madingley. The 1949 conference was devoted to a consideration of 'Physiological mechanisms in animal behaviour' and brought together for the first time leading representatives of animal behaviour study in Britain, continental Europe and North America. It inspired much new research in the 1950s and helped make ethology respectable and strong. To enable ethological research to develop with international cohesion, Thorpe directed the attention of the conference to the need to agree on the meaning of a number of ethological terms such as reflex, instinct, drive, appetitive behaviour, fixed action pattern, displacement activity, releaser, learning and imprinting. Greater progress would be made with a common theory and technical language.[69]

At Madingley, as was mentioned above, ethological work was soon well under way and in their survey Broadhurst and Martin recorded that it included studies of imprinting in birds,[70] of the determinants of nest building in the canary,[71] of the social behaviour[72] and response to predators[73] among various species of birds, and of the inheritance of patterns of song in chaffinches[74] and doves. The field station also established a colony of rhesus monkeys in their own building in semi-outdoor conditions, and one of the researches planned related to the development of vocal communication in that species. The Sub-Department of Animal Behaviour won support from the Josiah Macy Foundation, and in 1960 the Nuffield and Rockefeller Foundations funded a new laboratory. Thorpe was made a Reader in 1959 and elected into a personal chair in 1966, receiving much support from Carl Pantin (Professor of Zoology).

When Cyril Burt vacated the chair of psychology at University College, London in 1950, his successor, R.W.Russell, was ready to strike out into fresh fields, particularly into that of animal psychology. Russell was appointed from the U.S.A. and therefore

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[69]Durant, J.R. (1986b) op. cit.
[70]Hinde, R.A., Thorpe, W.H. and Vince, M.A. (1956) The following responses of young coots and moorhens. *Behaviour*, 9: 214-42.
[71]Hinde, R.A. and Warren, R.P. (1959) The effect of nest building on later reproductive behaviour in domesticated canaries. *Animal Behaviour*, 7: 35-41.
[72]Marler, P. (1957) Studies of fighting in chaffinches: 4. Appetitive and consummatory behaviour. *British Journal of Animal Behaviour*, 5: 29-37; Andrew, R.J. (1956) Fear responses in Emberiza spp. *British Journal of Animal Behaviour*, 4: 125-32.
[73]Hinde, R.A. (1954) Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (Fringilla coelebs): II. The waning of the response. *Proceedings of the Royal Society (B)*, 142: 331-58.
[74]Thorpe, W.H. (1958) The learning of song patterns by birds with especial reference to the song of the chaffinch (Fringilla coelebs). *Ibis*, 100: 535-71.

brought another tradition to bear on British work. Largely due to Russell, the University of London began to hold pride of place in the revival of interest in, and establishment of facilities for, the study of animal psychology. H.J.Eysenck had invited Russell to England in 1949 to establish the Animal Psychology Laboratory of the Institute of Psychiatry, and on his appointment in 1950 as Professor of Psychology at University College, London, he founded a second animal laboratory there. (Birkbeck College was also soon to accommodate one.)[75] The size of the staff at University College soon greatly increased, and by 1954 the Department, already housed in several different parts of the College, was about to move into new premises.[76] By 1960, the animal laboratories in the psychology and pharmacology departments were maintaining colonies of rats for a variety of purposes. From their survey, Broadhurst and Martin established that a Medical Research Council Unit in the Department of Psychology was primarily concerned with the relationship of behaviour to changes in body chemistry, especially as a result of chronic, minute doses of toxic agents.[77] The effects of drugs on behaviour[78] and of various environmental conditions were studied in both departments.[79] Other investigations in the Department of Psychology included the determination of the threshold for electric shock in the rat,[80] and of endocrine differences between the selected strains of rats from the Institute of Psychiatry.[81] Studies were made at University College by workers in the Department of Psychology on innate fear in ducks.[82] Work on the effects of brain lesions on conditioned responses in the octopus by workers in the Departments of Anatomy and Zoology[83] represented some of the early stages of neuroscience.

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[75]Broadhurst, P.L. and Martin, I. (1961b) op. cit.
[76]Flugel, J.C. (1954) A hundred years or so of psychology at University College, London. *Bulletin of the British Psychological Society*, 23: 21-31.
[77]Khairy, M. (1959) Changes in behaviour associated with a nervous system poison (D.D.T.). *Quarterly Journal of Experimental Psychology*, 11: 84-91.
[78]Glow, P.H. (1959) The blocking effect of benactyzine hydrochloride on a behaviour disturbance induced with lysergic acid diethylamide. *British Journal of Psychology*, 50: 338-48; Watson, R.H.J. and Steinberg, H. (1959) Effects of drugs on hyperglycaemia induced by stress in rats. In: Bradley, P.B., Deniker, P. and Radouco-Thomas, C. (eds) (1959) *Neuro-psychopharmacology*. Amsterdam: Elsevier.
[79]Andjus, R.K., Knopfelmacher, F., Russell, R.W. and Smith, A.U. (1956) Some effects of severe hypothermia on learning and retention. *Quarterly Journal of Experimental Psychology*, 8: 15-23; Steinberg, H. and Watson, R.H.J. (1959) Chlorpromazine inhibition of reactions of rats to unfamiliar surroundings. *Journal of Physiology*, 147: 20-22P.
[80]Green, R.T. (1958) Threshold for electric shock of the laboratory rat. *Animal Behaviour*, 6: 72-6.
[81]Watson, R.H.J. (1960) Constitutional differences between two strains of rats with different behavioural characteristics. *Advances in Psychosomatic Medicine*, 1: 160-5.
[82]Melzack, R., Penick, E. and Beckett, A. (1959) The problem of 'innate fear' of the hawk shape: an experimental study with mallard ducks. *Journal of Comparative and Physiological Psychology*, 52: 694-8.
[83]Boycott, B.B. and Young, J.Z. (1957) Effects of interference with the vertical lobe on visual discriminations in octopus vulgaris lamarck. *Proceedings of the Royal Society (B)*, 146: 439-59.

The well-equipped animal laboratory in the Department of Psychology at Birkbeck College maintained a colony of rats principally used in a series of experiments on conditioning and extinction,[84] especially exploring light as a reinforcer.[85] Work in 1960 was concerned with the parameters of operant behaviour in rats and pigeons, and a study of the behaviour of the jackdaw was in progress. Birkbeck College was noteworthy because undergraduates spent a term in the laboratory doing conditioning work with rats.[86] The behavioural work in the Department of Zoology was mostly concerned with the study of insects, especially in relation to the effects of acclimatization, and the genetics of their behaviour. Comparison of some aspects of courtship behaviour in Drosophila was being made with that in black-headed gulls.[87] At the Anti-locust Research Centre in London the behaviour of certain species of grasshopper was studied.[88] Meanwhile at Bedford College, London, the Psychology Department maintained a colony of hamsters used for studies of social dominance[89] in relation to the genetic composition of sub-strains. Work in progress in 1960 sought to relate these differences to physiological variables, and to investigate visual discrimination.

According to Broadhurst and Martin, by 1960 London could be said to be the centre of animal psychology in the more American tradition.[90] Broadhurst himself adopted a somewhat behaviourist approach to research.[91] In the Institute of Psychiatry, a

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[84]Hurwitz, H.M.B. (1957) Periodicity of response in operant conditioning. *Quarterly Journal of Experimental Psychology*, 9: 177-84.

[85]Hurwitz, H.M.B. (1956) Conditioned response in rats reinforced by light. *British Journal of Animal Behaviour*, 4: 31-3; Hurwitz, H.M.B. and Appel, J.B. (1959) Light-onset reinforcement as a function of the light-dark maintenance schedule for the hooded rat. *Journal of Comparative and Physiological Psychology*, 52: 710-12; Stewart, J. (1960) Reinforcing effects of light as a function of intensity and reinforcement schedule. *Journal of Comparative and Physiological Psychology*, 53: 187.

[86]Broadhurst, P.L. and Martin, I. (1961b) op. cit.

[87]Weidmann, U. (1956) Observations and experiments on egg-laying in the black-headed gull (Larus ridibundus L.). *British Journal of Animal Behaviour*, 4: 150-61.

[88]Haskell, P.T. (1960) Stridulation and associated behaviour in certain orthoptera: 3. The influence of the gonads. *Animal Behaviour*, 8: 76-81.

[89]Lawlor, M.M. (1956) Hereditary determinants of social dominance in the golden hamster. *British Journal of Animal Behaviour*, 4: 75-6.

[90]Broadhurst, P.L. and Martin, I. (1961a) op. cit.

[91]'The animal may seem sad or happy or angry, but we cannot infer that this is the case from the way we ourselves might feel in the same situation. To do so is to indulge in anthropomorphism - seeing man's shape in all things - and this is the cardinal crime for the animal observer. It may be that we are right in thinking the animal is sad or happy or angry, but the only thing we can know with certainty is what it *does* - how it behaves ... the conclusions the scientist draws will be more tentative for a given number of subjects in the field than they would be for the same number of subjects studied in the laboratory, where the possibly disturbing factors due to heredity and previous environment are controlled ... the less variability of response encountered the smaller the sample you need to study.' Broadhurst, P.L. (1963a) *The science of animal behaviour*. Harmondsworth, Middlesex: Pelican Books, pp.12 & 45.

postgraduate school of the University of London, his animal psychology laboratory housed a colony of about 1,000 rats including five pure-bred strains and two others established by divergent selection for emotional reactivity. Much of the activity of the laboratory at the time was centred around the use of these strains and was concerned with the nature and inheritance of emotional reactivity in the rat using observational[92] and conditioning[93] methods. A second area of research was in psychopharmacology[94] and a third in various aspects of learning.[95] Investigations in 1960 included the study of the interaction of genetic and ontogenetic factors as determinants of adult behaviour, and study of various aspects of drive - its summation and interaction with habit strength. The University of London was also a centre for other work on animal behaviour carried out by the departments of zoology, physiology etc.; for example, at the Institute of Neurology (National Hospital), where monkeys from a primate colony were used in discrimination problems and to test various theories of learning;[96] at the Royal Veterinary College Physiology Department where work on the affective behaviour of domesticated animals was examined, and studies were made on the taste thresholds of cows and goats;[97] and at Queen Mary College, where the Department of Nutrition collaborated with the Medical Research Council Unit, University College, in studying the effect of dietary deficiencies on behaviour.[98] The Department of Zoology of Queen Mary College was primarily concerned with the behaviour of marine invertebrates, e.g. the winkle,[99] in relation to their habitat.[100] At the Pharmacology Department of the London Hospital Medical College, Herxheimer worked on taste preference in rats.[101]

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[92]Broadhurst, P.L. (1960) Experiments in psychogenetics: applications of biometrical genetics to the inheritance of behaviour. In: Eysenck, H.J. (ed.) (1960) *Experiments in personality. Vol. I, Psychogenetics & psychopharmacology*. London: Routledge & Kegan Paul.
[93]Singh, S.D. (1959) Conditioned emotional response in the rat: I. Constitutional and situational determinants. *Journal of Comparative and Physiological Psychology*, 52: 574-8.
[94]Sinha, S.N., Franks, C.M. and Broadhurst, P.L. (1958) The effect of a stimulant and a depressant drug on a measure of reactive inhibition. *Journal of Experimental Psychology*, 56: 349-54.
[95]Broadhurst, P.L. (1957) Emotionality and the Yerkes-Dodson law. *Journal of Experimental Psychology*, 54: 345-52; Kendrick, D.C. (1958) Inhibition with reinforcement (conditioned inhibition). *Journal of Experimental Psychology*, 56: 313-8.
[96]Ettlinger, G. (1960) Discrimination learning theory: excitory vs inhibitory tendencies in monkeys. *Quarterly Journal of Experimental Psychology*, 12: 41-4.
[97]Bell, F.R. (1959) Preference thresholds for taste discrimination in goats. *Journal of Agricultural Science*, 52: 125-8.
[98]Khairy, M., Russell, R.W. and Yudkin, J. (1957) Some effects of thiamine deficiency and reduced caloric intake on avoidance training and on reactions to conflict. *Quarterly Journal of Experimental Psychology*, 9: 190-205.
[99]Newell, G.E. (1958) An experimental analysis of the behaviour of Littorina littorea (L.) under natural conditions and in the laboratory. *Journal of the Marine Biological Association of the United Kingdom*, 37: 241-66.
[100]Broadhurst, P.L. and Martin, I. (1961b) op. cit.
[101]Herxheimer, A. and Woodbury, D.M. (1960) The effect of desoxycorticosterone on salt and sucrose taste preference thresholds and drinking behaviour in rats. *Journal of Physiology*, 151:

In late 1939 it was proposed that a diploma be instituted at Oxford University for those who sought preparatory training in psychology, and this was established in 1941, requiring a year's course in general and experimental psychology with practical work and a special subject. In 1943 the Committee for Psychology raised the question of an Honours school, and the following year the Institute of Experimental Psychology re-opened, after its cessation of activities, because of the war, in 1942. Teaching and research at the Institute under Stephenson and Zangwill resumed in October 1945, through the valuable assistance of J.L.King, and proposals were presented for a final honours school of psychology, philosophy and physiology. In the meantime, in the light of the prospect of a chair and full status for the subject, two lectureships were established, R.C.Oldfield and B.Babington Smith being appointed in 1946. Many at Oxford remained unenthusiastic about the elevation of the subject of psychology.[102] 'Psychology at Oxford in 1947 had evolved to the stage of proposals for a chair and an honours school via the customary interaction between liberal - and often well-informed - supporting interests, and a conservative opposition somewhat buttressed by selective misconception ... The resulting compromise - that undergraduates must read psychology in combination with either philosophy or physiology - was a good and viable starting point.'[103] In 1949, the Institute, in which all the psychological teaching for the final honours school had now to be carried out, and which had also to accommodate six staff, about ten research students and an expanding library, occupied the same premises as before, at St Giles School, 34 Banbury Road. A hut containing eight small rooms had been added in 1947, and it is possible that space was so scarce that a disused, detached lavatory building was taken over and converted into a small research room.[104] Rats were forbidden access to the premises by the City Council and had to be kept in another department for experimental use. Oldfield states that at this time there was talk of installing a formicarium (for David Vowles, who was working at Reading), and also that medical colleagues enabled the psychologists to carry out psycho-pathological research with a neurological orientation.

The situation at Oxford after 1940 did not therefore at first permit its psychological staff to exercise much influence in the study of animal behaviour. In 1918, George Humphrey had gone to Harvard where he worked for a Ph.D. He was greatly

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252-60.

[102]Some report of the discussions in Congregation relating to the establishment of the Chair and Honours School is to be found in various numbers of the *Oxford Magazine* for the academic year 1946-7.

[103]Oldfield, R.C. (1966) Obituary: George Humphrey, 1889-1966. *Bulletin of the British Psychological Society*, 19, 65: 37-8.

[104]Oldfield, R.C. (1950) Psychology in Oxford 1898-1949, Parts 1 & 2. *Bulletin of the British Psychological Society*, 1: 345-53 & 382-7.

influenced during this period by Raymond Dodge and W.F.Dearborn, and the results of his Harvard experiences can be seen in a lasting concern with conditioning and with laboratory techniques for research on perception. In 1947, he was Dominion Fellow at St John's College, Cambridge, and in the same year went to Oxford as its first Professor of Psychology.[105] It is easy to imagine Humphrey's frustration after his arrival to occupy the new chair in 1947. Returning from Canada and the atmosphere and opportunity of more research in the American tradition, he found it difficult at Oxford to foster and increase experimental work in the animal field. Danziger[106] recalls: 'George Humphrey had done quite a bit of animal experimentation in his time, but by the time I knew him (1949) this was no longer a major interest of his. He had tried to continue his work on audiogenic seizures in rats at Oxford, but there were problems about licensing. I remember that people outside the discipline of psychology had expressed ethical concerns about audiogenic seizures.'[107] Oldfield[108] continues: 'Even with a growing undergraduate demand and an increase in research, psychology [at Oxford] found itself behind the march of the big battalions so far as provision of buildings and staff were concerned. Even this may have proved as well in the long run, for the subsequent expansion went far beyond what could conceivably have been granted in terms of new building by 1956', when Humphrey retired back to Cambridge, to be replaced by Oldfield. 'But the University's failure to achieve any amelioration of increasingly overcrowded working conditions was a bitter disappointment to Humphrey, and laid a heavy burden on him. This he successfully bore, and to such good effect that during his tenure Oxford became outstanding in psychology for the quality of its work and the distinction of those who went out to teaching and research posts elsewhere'. As for Oldfield, 'although never perhaps wholly at his ease in Oxford', he 'succeeded strikingly in transforming what had been a small and relatively insignificant subject, still regarded in some quarters with ill-concealed disdain, into a widely accepted and flourishing Honours School'.[109] He was also a founder member of the Experimental Psychology Group, of which he became President from 1956 to 1957, and was the first editor of the *Quarterly Journal of Experimental Psychology*. In 1960, he was President of Section J (Psychology) of the British Association for the Advancement of Science.

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[105]Argyle, M. (1966) Obituary: George Humphrey, 1889-1966. *Bulletin of the British Psychological Society*, 19, 65: 35-7.
[106]Danziger, K. (1987) Personal communication, 19 January.
[107]In the carrying out of his own research, on the operation of an acquired drive in satiated rats, Danziger recalls: 'Of course, at that time [1949-1951] the Institute had no facilities for animal work, so I had to arrange to do my work at the Laboratory for Human Nutrition.'
[108]Oldfield, R.C. (1966) op. cit.
[109]Zangwill, O.L. (1972a) Obituary: R.C.Oldfield, 1909-1972. *Bulletin of the British Psychological Society*, 25: 313-4.

By 1960, work at the Institute had been especially concerned with theory[110] as exemplified by the behaviour of rats in respect of drive discrimination and extinction[111] as well as with the analysis of motivational parameters.[112] Sutherland's work on the nervous control of behaviour in the octopus led to the formulation of a theory on the discrimination of visual shapes.[113] A study of inheritance of sexual behaviour in Drosophila was also carried out[114] and progressed at Edinburgh.[115] The ethological work at Oxford originated from the Department of Zoology and the Institute of Field Ornithology, and much academic collaboration began to take shape there with the psychologists. In the late 1950s as an undergraduate research assistant N.J.Mackintosh had worked for his tutor, Stuart Sutherland, on octopus both in Oxford and Naples. He recalls that a fellow research student in psychology, David McFarland, had a degree in zoology, that they all grew to know the students in Tinbergen's ethology group and shared their interests.[116] For several years into the early 1960s Mackintosh then taught (along with Tinbergen) an introductory course in comparative psychology and ethology to first year psychology undergraduates. By this time Oxford had become the centre for much work on instinctual responses in several species, particularly the stickleback[117] and the gull.[118]

The climate for ethology after the Second World War was especially good at Oxford, as can be seen in the enthusiastic description of developments there given by Professor A.C.Hardy to Section D of the British Association for the Advancement of Science.[119] He referred to the establishment, in July 1947, as a full university department, of the Department of Zoological Field Studies, the first in the world, whose objects were 'the

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110 Deutsch, J.A. (1956) A theory of insight, reasoning and latent learning. *British Journal of Psychology*, 47: 115-25.
111 Deutsch, J.A. and Clarkson, J.K. (1959) A test of the neo-behaviouristic theory of extinction. *Quarterly Journal of Experimental Psychology*, 11: 143-9.
112 Deutsch, J.A. and Jones, A.D. (1960) Diluted water: an explanation of the rat's preference for saline. *Journal of Comparative and Physiological Psychology*, 53: 122-7.
113 Sutherland, N.S. (1960) Visual discrimination of orientation by octopus: mirror images. *British Journal of Psychology*, 51: 9-18. N.J.Mackintosh notes that the work at Oxford and Naples was originally under the auspices of J.Z.Young, who had developed training procedures for studying discrimination learning, the research being on perception (pattern discrimination) rather than on learning as such. Sutherland's other interests, in animal learning theory, were related to those of Deutsch. Mackintosh, N.J. (1986) Personal communication, 10 December.
114 Bastock, M. (1956) A gene mutation which changes a behaviour pattern. *Evolution*, 10: 421-39.
115 Manning, A. (1959) The sexual isolation between Drosophila melanogaster and Drosophila simulans. *Animal Behaviour*, 7: 60-5.
116 Mackintosh, N.J. (1986) ibid.
117 Hoogland, R., Morris, D. and Tinbergen, N. (1956-7) The spines of sticklebacks (Gasterosteus and Pygosteus) as a means of defence against predators (Perca and Esox). *Behaviour*, 10: 205, 236.
118 Tinbergen, N. (1959) Comparative studies of the behaviour of gulls (Laridae): a progress report. *Behaviour*, 15: 1-70; (1960) The evolution of behaviour in gulls. *Scientific American*, 203: 118-30.
119 Hardy, A.C. (1949) Zoology outside the laboratory. *The Advancement of Science*, VI, 23: 213-23.

study of animals in nature: their ecology, behaviour and evolution'. This new department had been formed by combining the Bureau of Animal Population (founder-director, Charles Elton, whom Hardy described as a founder also of terrestrial animal ecology itself),[120] and the Edward Grey Institute of Field Ornithology (director, David Lack); and, linked with the Department of Zoology and Comparative Anatomy, it now came under Hardy as Linacre Professor. Laboratory and field studies in zoology were therefore now co-ordinated, and in 1947 a field station was established on the Wytham Estate, whose woodlands the university gave over to biological studies, with training courses (from 1948 under Charles Elton) as for those at Plymouth and other coastal laboratories in marine biology.

Tinbergen had a particularly influential effect at Oxford, where he had accepted a lectureship in animal behaviour in preference to the chair he had been offered at Leiden.

> Oxford was strong in the kinds of evolutionary and ecological interests that resonated with his kind of ethology. He had much in common, intellectually, with such people as E.B.Ford and Arthur Cain, David Lack and Charles Elton. They encouraged and reinforced his concern with questions about the evolution and adaptive significance of behaviour. Oxford ethologists came to be involved with such questions more actively and more exclusively than perhaps any other comparable group in the world. Many of the studies that Tinbergen instigated at Oxford were continuations of those with which he had been involved at Leiden. For example, experimental study of protective coloration in insects continued in David Blest's work on the 'eye-spot' displays of butterflies and moths; and stickleback studies were carried on by Desmond Morris, Fae Hall, Beatrice Tugendhat and others right up to the work of David Wilz in the late 1960s. Gull studies expanded in an ambitious programme covering numerous species and kinds of problem, even reaching out to take in terns and skuas. Among the people involved in this work were Martin Moynihan, Rita and Uli Weidmann, Michael and Esther Cullen, Gilbert Manley, Colin Beer, Hans Kruuk, Ian Patterson, Monica Impekoven, Heather McLannahan, Michael and Barbara MacRoberts, and Larry Schaffer. A new departure was the comparative and genetic study of behaviour in Drosophila species, to

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[120]Elton acknowledged the part played by Julian Huxley in a letter to him of December 1970: 'It was mainly you and your teachings and later your books that kept my interest in evolution alive ... I had meant to say publicly [on receipt of the Royal Society Darwin Medal] how much I owed to you in the difficult early days of my ecological work [- in the early 1920s ecology was a new subject, not fully approved of by 'classical' zoologists, who thought more about the anatomical structure of dead animals than what they did when alive, or their relations with their environment -], for encouragement of my research and also of the expression of my ideas.' Huxley, J.S. (1970) *Memories*, vols 1 and 2. London: George Allen and Unwin Ltd, p.241.

> which Margaret Bastock, Aubrey Manning, Stella Crossley, Richard Brown and others contributed. Robert Hinde, although not officially a member of Tinbergen's group, saw enough of it - and of Tinbergen himself - to become an ethologist in his Oxford doctoral research on the behaviour of Great Tits. The same species was later studied by Nick Blurton Jones, who went into human ethology after completing his doctorate. Contact with Tinbergen's group influenced W.M.S.Russell's work on Xenopus. Brian Nelson brought the gannets of Bass Rock, and then the gannets and boobies of the world, within the scope of the comparative ethological approach in work analogous to that on gulls.[121]

A key topic at the joint Institute for the Study of Animal Behaviour / Society of Experimental Biology conference at Cambridge in 1949 had been instinct, and it was on this occasion that Lorenz explained to an English-speaking audience his famous 'psycho-hydraulic' model of instinct, designed to explain the operation of the proposed 'innate releasing mechanism'. This model inspired a great deal of research in the 1950s and 1960s, particularly in the modified form which Tinbergen presented in *The study of instinct* in 1951.[122] In this highly influential book, which was the first comprehensive work on ethology in English, Tinbergen outlined four questions that ethology seeks to answer. The first three have to do with causes of behaviour and the fourth with its function. Thus, the ethologist seeks at one level the physiological mechanisms underlying observed behaviour; at another, the ontogeny of behaviour, or its development in the individual; at a third, the phylogeny or evolutionary development of behaviour; and fourthly, the function or 'biological significance' of the behaviour in question. These questions are still guidelines for ethology, though the original classic explanatory system of the 1930s and 1940s has since been modified.[123]

One day in May 1911 at Reading, he claimed, A.W.Wolters had been asked to present plans 'the following morning' for a psychological laboratory to form part of a new building for philosophy. He recalls that the plans were prepared at once, but were considerably modified by the time his department actually entered its new building in January 1942, leaving the philosophers in their own premises. Reading University had suffered for a long time from financial difficulties, but in 1942 its new laboratory was designed especially for psychology - possibly the only one in England besides the Cambridge laboratory, and much envied at the time. Wolters regarded the

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121 Baerends, G. et al. (eds) (1975) *Function and evolution in behaviour: essays in honour of Professor Niko Tinbergen, F.R.S.* Oxford: Clarendon Press.

122 Durant, J.R. (1986a) From amateur naturalist to professional scientist. *New Scientist*, 24 July, pp. 41-4.

123 Asquith, P.J. (1981) op. cit., pp.70-1.

experimental element of the undergraduate course as an unsolved problem, since comprehensive coverage of subjects would lead to superficiality and there was not enough time for intensive experimental work to be completed and illustrate lectures: 'We meet this difficulty to some extent by giving a comprehensive course, with the additional requirement that candidates shall present a thesis embodying continued experimentation as an integral part of the degree examination. The aim was to ensure that all students should get the feel of real experimentation, and it would have been sufficient had they imitated some published research. Candidates have become very independent and adventurous ...'[124] M.D.Vernon commented of Wolters: 'It is interesting to note that one of his last tasks before retiring [in 1950] has been the preparation of plans for a new and even more commodious laboratory to be included in the new University which will be built one day on the outskirts of Reading.'[125] By 1960 the Psychology Department was keeping insects and small fish, and the research work was concerned with brain mechanisms and vision in insects, especially in ants[126] and locusts.[127]

Broadhurst and Martin record that by 1960 at Birmingham, several departments were concerned with animal behaviour. In the Department of Anatomy, study was concentrated on the influence of hormones, especially thyroid hormones, on the nervous system of the rat,[128] and also on work on the olfactory acuity of the rat[129] and the dog.[130] In the Department of Experimental Psychiatry, psychopharmacological studies were carried out using several species of animals to investigate the influence of drugs on behaviour, with particular reference to the reticular system.[131] The Pharmacology Department was especially concerned with the analysis of exploratory behaviour in the rat,[132] and with social influences on the effects of drugs in rodents[133]

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[124] Wolters, A.W. (1948) An autobiography. *Occupational Psychology*, 22: 180-9.
[125] Vernon, M.D. (1950) Albert William Wolters. *Quarterly Bulletin of the British Psychological Society*, 1, 10: 379-81.
[126] Vowles, D.M. (1958) The perceptual world of ants. *Animal Behaviour*, 6: 115-6.
[127] Wallace, G.K. (1959) Visual scanning in the desert locust (Schistocerca gregaria forskal). *Journal of Experimental Biology*, 36: 512-25.
[128] Eayrs, J.T. (1959) The status of the thyroid gland in relation to the development of the nervous system. *Animal Behaviour*, 7: 1-17.
[129] Moulton, D.G. (1960) Studies in olfactory acuity: 5. The comparative olfactory sensitivity of pigmented and albino rats. *Animal Behaviour*, 8: 129-33.
[130] Moulton, D.G., Ashton, E.H. and Eayrs, J.T. (1960) Studies in olfactory acuity: 4. Relative detectability of n-Aliphatic acids by the dog. *Animal Behaviour*, 8: 117-28.
[131] Bradley, P.B. (1959) Methods and analysis of drug-induced behaviour in animals. In: Bradley, P.B., Deniker, P. and Radouco-Thomas, C. (eds) (1959) *Neuro-psychopharmacology*. Amsterdam: Elsevier; Key, B.J. and Bradley, P.B. (1960) The effects of drugs on conditioning and habituation to arousal stimuli in animals. *Psychopharmacologia*, 1: 450-62.
[132] Mead, A.P. (1960) A quantitative method for the analysis of exploratory behaviour in the rat. *Animal Behaviour*, 8: 19-31.

as well as the evolutionary significance of seizures.[134] Chance carried out one of the few studies at the time of social behaviour in primates.[135] Danziger[136] comments: 'During that period [1949-1951] the influence of one or two people outside psychology was very much more important than anything within the discipline. Dr Chance of Birmingham was doing animal work that aroused interest among some of the younger generation ...' Furthermore, Chance himself had undertaken earlier work for the Glaxo laboratories (as referred to in the *Bulletin of Animal Behaviour* in 1948), and during the 1950s animal colonies for behavioural work became established in the research departments of other pharmaceutical companies in Britain, but by the end of the decade few results had been published.[137]

Broadhurst and Martin noted that the Psychology Department at Sheffield University used the selected strains of rats from the Institute of Psychiatry in London in a study of exploratory behaviour,[138] and at Liverpool the School of Tropical Medicine was concerned with the effects of parasitic diseases on psychological functioning in the rat.[139] At Durham University the Psychology Department kept chickens as well as rats: using laboratory techniques, the 'following' response in young chicks (imprinting) was subjected to analysis.[140] In the Poultry Research Centre at Edinburgh, the determinants of sexual drive in chickens were investigated;[141] and at Glasgow in the Zoology Department wild rats were extensively studied, for example in respect of their social behaviour,[142] and their response to stress.[143]

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[133]Chance, M.R.A. (1956a) Environmental factors influencing gonadotrophin assay in the rat. *Nature*, 177: 228-9.
[134]Chance, M.R.A. (1957) The role of convulsions in behaviour. *Behavioral Science*, 2: 30-40.
[135]Chance, M.R.A. (1956b) Social structure of a colony of Macaca mulatta. *British Journal of Animal Behaviour*, 4: 1-13; also Hall, K.R.L. (1960) A field study of the behaviour of baboons. *Bulletin of the British Psychological Society*, 40: 3A.
[136]Danziger, K. (1987) Personal communication, 19 January.
[137]Ryall, R.W. (1958) Effect of drugs on emotional behaviour in rats. *Nature*, 182: 1606-7. Cited by Broadhurst, P.L. and Martin, I. (1961b) op. cit.
[138]Stretch, R.G.A. (1960) Exploratory behaviour in the rat. *Nature*, 186: 454-6.
[139]Stretch, R.G.A., Stretch, S.J.E., Leytham, G.W.H. and Kershaw, W.E. (1960) The effects of schistosomiasis upon discrimination learning and activity in mice: I. An acute infection. *Annals of Tropical Medicine and Parasitology*, 54: 376-80.
[140]Salzen, E.A. and Sluckin, W. (1959) The incidence of the following responses and the duration of responsiveness in domestic fowl. *Animal Behaviour*, 7: 172-9; Smith, F.V. (1960) Towards definition of the stimulus situation for the approach response in the domestic chick. *Animal Behaviour*, 8: 197-200.
[141]Wood-Gush, D.G.M. (1960) A study of sex drive of two strains of cockerels through three generations. *Animal Behaviour*, 8: 43-53.
[142]Barnett, S.A. (1960) Social behaviour among tame rats and among wild white hybrids. *Proceedings of the Zoological Society of London*, 134: 611-21.
[143]Barnett, S.A., Eaton, J.C. and McCallum, H.M. (1960) Physiological effects of 'social stress' in wild rats: II. Liver glycogen and blood glucose. *Journal of Psychosomatic Research*, 4: 251-60.

Conclusion

An assessment made by P.L.Broadhurst indicates the nature of the study of animal behaviour in the years leading up to 1960:

> The pattern of research is ... too fragmentary to allow any general trends in it to be discerned. Perhaps it may be said that, judging from recent published work on the psychological side, there is something of an interest in work on exploratory behaviour in the rat as well as a revival of interest among both psychologists and comparative ethologists in the effects on the nervous system of brain lesions, using species not usually associated with this type of work, such as birds and octopus. We know of no current work with animals in the strictly Pavlovian style, for example using salivary reflexes in dogs. The traditionally British emphasis on the study of individual differences combined with an interest in hereditary determinants is exemplified in some of the research emanating from London University. The Continental ethological approach has taken root firmly in Britain ... [with] Oxford and Cambridge the centres of ethological studies ... and has produced some notable research work. It has changed in the process and now shows greater experimental and analytical sophistication than was sometimes displayed in its original setting.[144]

From 1940 to 1960 the development of professional organizations and the establishment and growth of centres of research are reflected in an increase in the number and size of journals, in the number and variety of authors (some of whose contributions were regular and occasionally serialized), in the substance and scientific quality of their articles, and, finally, in the wide-ranging and imaginative nature of the work undertaken.

At the conclusion of this phase in the experimental study of animal behaviour, Donald Broadbent, then at the Applied Psychology Unit of the Medical Research Council, Cambridge, reviewed the status of a modern behavioural approach to the subject and attempted to emphasize its importance as providing: necessary objectivity; scope for recognition of autonomous behaviour in organisms (as opposed to 'stereotyped actions laid down by heredity or stamped in by environment'); and evidence that there was capacity for flexible learning above rigid mechanistic behaviour. To this end he concentrated of necessity on American work, and the only significant reference he made to British work was to that of J.A.Deutsch. He acknowledged the neglect of species other than the rat, and of the study of innate, 'natural' behaviour, a neglect

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[144]Broadhurst, P.L. and Martin, I. (1961b) op. cit., pp.167 & 168.

which he felt would in future be corrected by an increased involvement by zoologists. He further recognized the growing need to involve physiologists in behavioural work, a need which would shortly be answered by the role neuroscience had to play in psychology, as when, for example, Deutsch began to introduce his servo analogies for the variation, rather than traditional rigidity, in behavioural response observable during the learning process. Broadbent himself believed that information entering the nervous system was 'filtered', not all of it producing a behavioural effect. His prognosis for experimental psychology was optimistic: 'At a rough guess, two hundred more years may bring the study of behaviour up to the level which physics reached in Newton's time'.[145]

[145]Broadbent, D.E. (1961) *Behaviour*. London: Eyre and Spottiswoode.

CHAPTER 6

EXPANSION AND DEVELOPMENT AFTER 1960

Introduction

The report of the Trend Committee in 1963[1] had resulted partly from the admission of the Advisory Council on Scientific Policy that its task had outgrown it and that it lacked the machinery for arriving at decisions on major priorities, and in February 1964 a 'federal' Department of Education and Science was created, the government also announcing that it would implement most of the recommendations of the report. Under a new Labour government the Science and Technology Act of 1965 brought into being the Science Research Council and Natural Environment Research Council, as proposed by Trend, answerable to the Secretary of State of the DES, who was advised by a Council for [civil] Scientific Policy; and in October 1966 the Central Advisory Council for Science and Technology was created to advise the Cabinet.[2] In the 1960s a familiar issue was the relationship between pure and applied research, and the value, funding and cost-effectiveness of each. The Gibb-Zuckerman Report[3] of 1961 had suggested that pure research was better conducted in the freer academic environment of the university than the government research establishments which were tasked with solving specific problems. The Robbins Report[4] then proposed the expansion and re-organization of higher education and the development of existing and new institutions, with an increase in the general proportion of science and technology students.[5]

Coinciding with these developments was the intensification of science coverage in the broadcast media, for which subjects related to natural history were especially suited, and which tended not to be subject to the sometimes suspicious and critical comments of journalists affecting other areas of science in the post-war period. Individuals began

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[1]*Report of the Committee of Enquiry into the Organization of Civil Science*, under the chairmanship of Sir Burke Trend, Cmnd. 2171, October 1963. London: HMSO.
[2]Poole, J.B. and Andrews, K. (eds) (1972) *The government of science in Britain*. London: Weidenfeld and Nicolson, pp.160-1.
[3]Office of the Minister for Science (1961) *The Management and Control of Research and Development*. London: HMSO.
[4]*Report of the Committee on Higher Education*, under the chairmanship of Lord Robbins, Cmnd. 2154, October 1963. London: HMSO.
[5]Argles, M. (1964) *South Kensington to Robbins: an account of English technical and scientific education since 1851*. London: Longmans, p.145.

to become entrepreneurial in describing and popularizing their work, while in those sciences where there existed a strong component of common experience or of observation of commonly accessible phenomena, such as natural history, amateurs were still involved to an appreciable extent and represented a link between the professional scientists and the public. 'The participation of amateurs blurs the distinction between professional scientists, on the one hand, and the general public, on the other. Moreover, areas of science with extensive amateur participation are among those most heavily featured by the media,'[6] notably BBC2 which resulted eventually from the findings of the Pilkington Report in 1962. A science correspondent had been appointed by BBC television in 1959 'as a reflection of the increasing importance of science.'[7] At that point, scientists were enabled usually to present their information as authorities rather than as people whose activities might be questioned, and in 1963 a new television group, Feature and Science programmes, led the way to a three-fold increase in science coverage by the BBC through programmes such as 'Horizon,' which was charged with exploring the 'scientific attitude' and being 'more concerned with ideas and philosophies of science than with techniques, or even discoveries.'[8]

Studies in animal behaviour in Great Britain since 1960 have been characterized by a rapid, further diversification of work, an increase in the number of scientists to undertake it, and a growth in the quantity and variety of the centres of research from which they have published their findings. The experimental study of animal behaviour has also attracted further and more concentrated interest in those scientists who were employed by organizations other than universities with psychology departments. Research interests have been divided into programmes of work with a purely academic basis and into those with a requirement for the immediate application of practical research to specific problems such as brain injury or pest infestation. Psychology forged symbiotic links with other areas in which studies of animal behaviour could be useful. Anthropologists examined the evolution of human behaviour by reference to field studies of primates; neuroscientists linked behaviour patterns in animals with the organization and function of the central nervous system, and neuroendocrinologists added hormones to the equation especially to examine reproductive behaviour, aggression and stress; and the veterinary and agricultural sciences have increasingly drawn on and contributed to studies of animal behaviour for a variety of reasons, often economic or related to newly prominent and connected welfare issues. 'While

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[6]Jones, G., Connell, I. and Meadows, J. (1978) *The presentation of science by the media*. University of Leicester: Primary Communications Research Centre, p.24.
[7]BBC Handbook, 1960, p.22.
[8]Jones, G., Connell, I. and Meadows, J. (1978) op. cit., p.36.

differences in emphasis remain, a synthetic study of animal behaviour in which scientists of different backgrounds interact harmoniously appears to have come of age.'[9]

In the 1960s, the establishment of new universities with courses in psychology heightened teaching and research activity and generated a new supply of scientists for the following decades.[10] Beyond the university departments, the national requirement for more efficient and economic agricultural productivity intensified behavioural research connected with animal breeding and husbandry. The development of drugs and the growth in the attempts to tackle nervous diseases and injuries suggested that studies of animal behaviour be undertaken to ensure the safety or effectiveness of processes. Finally, industrial and economic pressures on the natural environment required urgent investigations of a variety of ecological processes, such as the movement of animal populations on the land and in the sea.

An account of the interests and output of university centres of research in 1960[11] reports rather simplistically that at that time the investigation of animal behaviour was undertaken mainly by zoologically-trained and field-orientated ethologists, or by rat-orientated, laboratory-based academic psychologists, now heavily influenced by traditional American methodology. This categorization reflected the contemporary perception of the two areas, which had only recently begun the first stages of co-operation. The ethologists had a background of naturalistic interest in a large number of different species, especially birds, and a concern for the study of the evolution of behaviour. As their work progressed, the two types of behavioural researcher began to share and borrow methods. The laboratory-based psychologist began to acknowledge the importance of the natural environment in affecting the behaviour of animals, and the ethologist often became attracted to the laboratory, or at least tempted to apply more rigid standards of design, measurement and analysis. By the early 1960s, the distinction between some of the work of ethological stations and psychological laboratories was becoming blurred, and explicit attempts were being made by those such as Hinde[12] to bridge the gap in outlook between them[13] as it

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[9] Dewsbury, D.A. (1978) *Comparative animal behaviour.* New York: McGraw-Hill Book Co., p.28.
[10] c.f. Hearnshaw, L.S. (1969) Psychology in Great Britain: an introductory historical essay. *Supplement to the Bulletin of the British Psychological Society*, 22: 3-9.
[11] Broadhurst, P.L. and Martin, I. (1961a) Comparative and physiological psychology in Britain 1960. *Bulletin of the British Psychological Society*, 45: 41-55; (1961b) The study of higher nervous activity in Britain. *Activitas Nervosa Superior*, 3: 164-76.
[12] e.g. Hinde, R.A. (1966) *Animal behaviour: a synthesis of ethology and comparative psychology.* New York: McGraw-Hill Book Co.
[13] Thorpe, W.H. and Zangwill, O.L. (eds) (1961) *Current problems in animal behaviour.* Cambridge:

became realized that animals' habits were learned within the constraints imposed by genes.[14] A *detente* between ethology and ecology has also led to the acceptance that the differences in social behaviour between closely related species can be better understood if the constraints of the environment and of the distribution of food are taken into account.[15]

The Animal Behaviour Research Group

A description of the work of the Animal Behaviour Research Group in the Department of Zoology at Oxford University, at a meeting of the Association for the Study of Animal Behaviour in July 1962, reveals a neat reconciliation within the Group of projects based in the field with those of the laboratory.[16] All projects served the Group's aim to study animal behaviour in the same way as other life processes were studied: 'to describe it as objectively as possible, and to ask four major questions, viz. (i) What is the survival value of the observed behaviour [function]? (ii) What is its causation [antecedent cause]? (iii) How does it develop in the individual [development]? and (iv) How has it evolved [evolution]? It is because of this biological approach to behaviour that we do not intend to become a separate institute but to remain a part of the Department of Zoology'. After establishment in 1949, the Group had decided that ethology would be doomed if it did not attempt to enter certain 'no-man's-lands' between it and sister disciplines, and so work was included on neurophysiological aspects of behaviour, ecology, genetics, evolution, and other areas when at opportune times the collaboration of specialists was possible. The Group developed with the material assistance of the University, the Agricultural Research Council, the Nuffield Foundation, the Ford Foundation, the Nature Conservancy, and the U.S.A.F. Office of Aerospace Research. By 1962 it consisted of the Reader in Animal Behaviour, three post-doctoral research workers in various grades, a secretary, and nine graduates working for the degree of D.Phil. Field work was carried out at Ravenglass, Cumberland, on communications in black-headed gulls (Mash); egg-shell

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University Press.

14. 'If a rapprochement has been reached between the American and European "schools," it is largely due to the personal and intellectual efforts of Thorpe and Hinde and their pre- and postdoctoral students (Peter Marler, Peter Klopfer, Patrick Bateson, John Fentress, among others).' Gottlieb, G. (1979) Comparative psychology and ethology. In: Hearst, E. (ed.) (1979) *The first century of experimental psychology*. Hillsdale, New Jersey: Lawrence Erlbaum Associates, p.167fn. Furthermore, between the late 1950s and the 1980s behaviourism began to decline in the USA and 'cognitive science' to emerge.

15. Sparks, J. (1982) *The discovery of animal behaviour*. London: Collins, p.274.

16. Tinbergen, N. (1963b) The work of the Animal Behaviour Research Group in the Department of Zoology, University of Oxford. *Animal Behaviour*, XI: 206-9.

removal and defence against predation by foxes, hedgehogs, carrion crows and herring gulls (Kruuk); and gullery spatial patterns (Patterson). At a second field base at Walney Island, Dr J.D.Delius and Dr R.G.B.Brown studied behaviour patterns of the herring gull and lesser black-headed gull with a view to later laboratory-based analysis of behavioural components using brain-stem stimulation. The third, temporary, field base was the Bass Rock, where, under the supervision of Dr J.M.Cullen, J.B. and J.Nelson studied the population and behaviour of the gannet. G.C.Phillips worked in both field and laboratory to test coloration, camouflage and survival value in gulls and terns. He tested Craik's theory of gull camouflage by sailing dark and light bird models over captive fish to test their reactions. In the laboratory, Cullen examined the effects of the drug benactyzine on the behaviour of three-spined sticklebacks. C.J.Henty studied the alleged crypsis of the banding pattern of Cepaea snails as a method of defence against the song-thrush, and the ontogeny of snail-smashing in thrushes. N.G. Blurton Jones was completing his account of a three-year study of the agonistic displays of the great tit and related species, while the mating behaviour of Drosophila was studied by R.G.B.Brown and by Mrs S.A.Crossley (nee Pearce), under the supervision of Mrs M.Manning (Dr M.Bastock).

From the 1930s to the 1950s ethologists had interpreted social behaviour in terms of interactions between individual organisms representative of species, and the role of groups and population biology was largely neglected[17] until its significance was revealed by studies of gulls, kittiwakes and terns by Tinbergen (1959), Esther Cullen (1957) and J.M.Cullen (1960). Attention now began to be given to factors essential to behavioural ecology: contrasts in seasonality and availability of food resources in relation to evolution of clutch size; parental behaviour; length of breeding season; and other features of reproductive behavioural biology.[18]

New university departments, research interests and undergraduate training

At the time that this well-developed programme was evolving under the direction of the securely established Oxford group, the very beginnings of brand new departments were taking shape elsewhere. The period 1960 to 1969 generally saw a rapid growth

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[17]But see Lack, D. (1954) *The natural regulation of animal numbers*. Oxford: Clarendon Press; and Fisher, J. (1954) Evolution and bird sociality. In: Huxley, J.S., Hardy, A.C. and Ford, E.B. (eds) (1954) *Evolution as a process*. London: Allen and Unwin.

[18]Crook, J.H. (1989) Introduction: Socioecological paradigms, evolution and history: perspectives for the 1990s. In: Standen, V. and Foley, R.A. (eds) (1989) *Comparative socioecology: the behavioural ecology of humans and other mammals*. Oxford: Blackwell, p.5.

of university departments, research outlets and professional posts, with a large increase in the number of students studying psychology in the universities. Twenty-one new chairs of psychology were established,[19] more than in the previous sixty years.[20] In 1960 there were 199 honours graduates; in 1967, 667. Books and broadcasts on psychological subjects encouraged general interest, so that 'during the 1960s psychology in Great Britain has begun to enter an entirely new phase in its development', and 'developments in social psychology have not been at the expense of the biological and comparative sides of psychology, which are, indeed, showing renewed strength ... a result largely of a blood transfusion from continental ethology, which has led to a renewed interest in animal behaviour, and a reforging of the links between psychologists and zoologists.'[21]

A process of mutual cross-fertilization between comparative psychology and zoological ethology was taking place at the end of the 1960s,[22] as a development from the weaker contacts existing earlier in the decade. However, the comparative psychologists of 1969 continued to concentrate on the study of regularities of behaviour in man and animals, as exemplified in different species; while the ethologists continued to attempt to clarify modes of behaviour and to identify the biological

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[19]Among significant new chairs were:
i) Aberdeen, second chair, 1965, J.R.Symons appointed.
ii) Birmingham, first chair, 1965, P.L.Broadhurst appointed.
iii) Bristol, chair in experimental psychology, 1969, J.Brown appointed.
iv) Dundee, first chair, 1968, S.Griew appointed.
v) Exeter, first chair, 1963, R.L.Reid appointed.
vi) Hull, first chair, 1962, A.D.B.Clarke appointed.
vii) Keele, first chair, 1962, I.M.L.Hunter appointed.
viii) Leicester, first chair, 1960, S.G.M.Lee appointed; personal chair, 1965, W.Sluckin appointed.
ix) Newcastle-upon-Tyne, first chair, 1966, J.Brown appointed; R.Davis appointed 1969.
x) Nottingham, first chair, 1960, W.J.H.Sprott appointed; C.I.Howarth appointed 1964.
xi) St Andrews, first chair, 1963; M.A.Jeeves appointed 1969.
xii) Sheffield, first chair, 1960, H.Kay appointed.
xiii) Southampton, first chair, 1964, G.B.Trasler appointed.
xiv) Stirling, first chair, 1966, P.McEwen appointed.
xv) Sussex, chair in experimental psychology, 1963; N.S.Sutherland appointed 1964.
xvi) University College of North Wales, Bangor, first chair, 1963, T.R.Miles appointed.
xvii) University College of Wales, Cardiff, first chair, 1961, G.Westby appointed.
xviii) University College of Wales, Swansea, first chair, 1965, C.E.M.Hansel appointed.
Some universities had, and others continued to have, a department of psychology without a professor; others only included psychology as part of a curriculum. Some technical colleges preparing students for external London degrees had large psychology departments: West Ham College of Technology had an undergraduate department in 1969 which was one of the largest in the country.
[20]Kenna, J.C. (1969) Chairs of psychology in British universities. *Supplement to the Bulletin of the British Psychological Society*, 22: 9-13.
[21]Hearnshaw, L.S. (1969) op. cit., pp.6,7 & 8.
[22]Sluckin, W. (1969) Animal behavioural and ethological work. *Supplement to the Bulletin of the British Psychological Society*, 22: 35-6.

functions of diverse behaviour patterns. Studies of animal learning (e.g. operant conditioning of rats and pigeons, at Nottingham, Hull, Reading and Exeter) were occupying much of the time of university psychological laboratories in the late 1960s. Discrimination learning by invertebrates and vertebrates was examined at Sussex, as were memory systems in invertebrates at University College, London. At Oxford and Reading much interest was shown in the motivation of hunger, thirst and curiosity.

According to Sluckin,[23] the developing field of study in British centres of research in 1969 was behaviour genetics (temporarily also known as psychogenetics). The fruit fly and rat were studied in Birmingham, London, Sheffield and Hull, in order to shed light on the interaction of the genetic and environmental determinants of behaviour. This was also the aim of research investigating lasting effects of various pre-natal and infantile experiences, at Belfast and Hull. Allied research into imprinting and other types of early learning enabled a merger of the ethological and comparative-psychological traditions, and was conducted at Cambridge, Aberdeen, Leicester, Durham and Sheffield. To attempt to explain human personality development, mother-infant interaction in monkeys living in groups was also studied at Cambridge, again combining ethology with psychology. Apart from pure ethology at Cambridge, Oxford and Glasgow, ethological research for psychological and psychiatric purposes was undertaken at Bristol, Birmingham, Leicester, Edinburgh and other universities.

In 1960, S.G.McK.Lee (1920-1973) took the first chair of psychology in the University of Leicester, as described in an obituary by W.Sluckin.[24] He built up a vigorous department with wide and varied research which became known primarily for its experimental and observational work with animals (which was not, however, Lee's own specialism). The department moved in 1968 to its own spacious building and also acquired, on the outskirts of Leicester in Oadby, a field station for the study of animal behaviour. At the field station, studies developed in its semi-natural environment of various aspects of behaviour of several wildfowl species. In the 1960s and 1970s the laboratory accommodated mice, rats, guinea pigs, ducklings, gerbils, hamsters, locusts, fruit-flies, kittens (fed from plastic bottles from a doll's outfit), fish, 10-18 month old babies, motion-sick subjects, and 11-year-old Wyggeston schoolboys at exam times. The major figure at Leicester at this time was Sluckin, who joined the department in 1960 after establishing a reputation with his colleague Eric Salzen at Durham for

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[23](1969) ibid.
[24]Sluckin, W. (1973) Obituary: S.G.McK.Lee, 1920-1973. *Bulletin of the British Psychological Society*, 26: 233.

studies of imprinting and early learning and which then extended to maternal bonding. Sluckin replaced Lee as head of department in 1973, having been editor of the *British Journal of Psychology* since 1967, and later became dean of the faculty of science.[25]

Vertebrates ranging from fish to monkeys were used for many types of experiment, e.g. social displays in fishes and birds, the development of bird song, of aggression, maternal behaviour etc. in mammals, and underlying physiological mechanisms. The fields of interest of the decade's more prolific investigators are set out in Appendix III. Physiological psychology itself, as the experimental study of the role of the central nervous system in behaviour, was flourishing at Cambridge, London, Oxford and Sussex, with considerable variety in the style and direction of research in these and other centres.[26]

In 1962, O.L.Zangwill had described the newly completed building for the Cambridge Psychological Laboratory.[27] In a sequel,[28] he commented on the way the facility was meeting pressures of use. Among misjudgements about workspace requirements was

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[25]Beech, J., Colley, A. and Colman, A. (1985) *The first twenty-five years of the psychology department at Leicester University*. Leicester University: Department of Psychology.
[26]Humphrey, N.K. (1969) Physiological psychology. *Supplement to the Bulletin of the British Psychological Society*, 22: 35. The areas of research and the people and places involved were as follows:
i) Perception, learning and memory in primates: Iversen and Latto at the Psychological Laboratory, Cambridge; Noble and Butler at the Department of Anatomy, University College, London; Ettlinger at the Maudsley Hospital, London; Weiskrantz, Cowey and Humphrey at the Institute of Experimental Psychology, Oxford; Oxbury at the University Laboratory of Physiology, Oxford.
ii) Attention and arousal: Grey-Walter and McCallum at the Burden Neurological Institute, Bristol; Oswald at the Department of Psychiatry, Edinburgh; Venables at Birkbeck College, London.
iii) Motivation: Broadhurst at the Department of Psychology, Birmingham; Vowles and Wright at the Department of Psychology, Edinburgh; Fitzsimons at the Department of Physiology, Cambridge; Prescott at the Sub-Department of Animal Behaviour, Cambridge; Herberg at the National Hospital, London; Michael at the Maudsley Hospital, London; McFarland at the Institute of Experimental Psychology, Oxford; Macphail and Oatley at the Department of Psychology, Sussex.
iv) Memory consolidation: Still at the Department of Psychology, Durham; Russell at the Department of Psychology, University College, London; Zinkin at the Institute of Experimental Psychology, Oxford.
v) Electrophysiology of sensory systems: Burns at the National Institute of Medical Research, London; Wall at the Department of Anatomy, University College, London; Horn at the Department of Anatomy, Cambridge; Muntz at the Department of Psychology, Sussex.
vi) Brain biochemistry: Rose at Imperial College, London; Smythies at the Department of Psychiatry, Edinburgh; Booth at the Department of Psychology, Sussex.
vii) Clinical neurology: Zangwill at the Psychological Laboratory, Cambridge; Warrington, Halliday, McFie and Pratt at the National Hospital, London; Piercy and Wyke at the Maida Vale Hospital, London; Newcombe, Whitty and Russell at the Churchill Hospital, Oxford.
[27]Zangwill, O.L. (1962) The Cambridge Psychological Laboratory. *Bulletin of the British Psychological Society*, 48: 22-4.
[28]Zangwill, O.L. (1968) News from the Cambridge Psychological Laboratory. *Bulletin of the British Psychological Society*, 21, 73: 233-4.

that concerning research testing rooms in the animal section, which turned out to be too large: two had to be divided, at great cost. But the new building was generally successful, and influenced the design of the Institute of Experimental Psychology at Oxford (under construction in 1968). Later, an extra floor was added, which helped with animal accommodation, undergraduate teaching, and research. In 1968 there were 185 undergraduates using the department, twelve research students and some Medical Research Council external staff.

R.C.Oldfield died in 1972, and his achievements were described in an obituary by O.L.Zangwill.[29] Oldfield had succeeded Humphrey as Professor of Psychology at Oxford in 1956, and during the following ten years did much to develop the work of the Institute of Experimental Psychology and to plan for its expansion in terms of staff, student numbers, and accommodation as especially represented by the new building for zoology and psychology, opened in 1971. 'As he saw it, psychology would be much better advised to attract the interest of able young men and women trained in the various fields of natural science than to set itself up as an exclusive and self-contained academic discipline.'[30]

The Monthly Report section of the *Bulletin of the British Psychological Society* announced for a brief period in the mid-1970s news of developments taking place in psychology departments around the country that sometimes concerned animal work.[31] At the Queen's University, Belfast, exchanges were planned with the psychological laboratory of the University of Brussels, grant-aided by the European Brain and Behaviour Training Organization: common interests included the development of behaviour in rodents. The Department of Psychology at Warwick University was established in October 1974, with thirty students and five staff. It was intended to increase these numbers to 200 and twenty respectively by 1979 and to provide animal facilities within two years, but no work on animal research had been published by 1980. Derrick Pritchatt,[32] in an article in the *Bulletin of the British Psychological Society* on comparative psychology as an undergraduate practical course, concluded that although the subject as a research field was already gaining ground in Britain, as an area of undergraduate study its acceptance was still minimal. However, he

[29]Zangwill, O.L. (1972a) Obituary: R.C.Oldfield, 1909-1972. *Bulletin of the British Psychological Society*, 25: 313-4.
[30]Zangwill, O.L. (1972b) Obituary notice: R.C.Oldfield, 1909-1972. *Quarterly Journal of Experimental Psychology*, 24: 375-7.
[31]e.g. vol.28, pp.120-1, 322-3, 453.
[32]Pritchatt, D. (1966) Comparative psychology as an undergraduate practical course. *Bulletin of the British Psychological Society*, 19, 65: 25-7.

described the use of invertebrates by psychology undergraduates at Leeds, and expected the trend to develop. Work with Protozoa could explain nervous threshold, summation, adaptation, fatigue, etc. Hydra, flatworms, earthworms, various insects, woodlice and Daphnia were also used to explain diversity in behaviour, for example in response to light stimuli; and to perform classical conditioning experiments, carried out to make longitudinal comparisons through the phyla by means of negative reinforcers, usually electric shock.

A number of articles in the *Bulletin of the British Psychological Society* discussed both training and the financing of research in British universities. C.R.Bell[33] noted that in 1966 not one of the six new universities in East Anglia, Essex, Kent, Lancaster, Warwick and York permitted graduation in psychology, or, except for sociology students at York, the taking of a course in psychology which was subsidiary to other courses. These universities had decided to delay the establishment of psychology departments, and in their prospectuses mentioned no immediate plans for introducing courses for psychology degrees. Bell attributes this problem to a misunderstanding of what psychology meant and what it could offer. Those British universities offering degree courses in psychology by 1975 were approached by the authors of a subsequent article[34] in order to assess topic areas in psychology as represented by the universities' examinations. A total sample of 2929 examination questions was obtained, and these were classified by the authors who were able then to carry out a frequency analysis. Animal behaviour and comparative psychology represented 17.9% of the biological category, which itself took up 23.5% of the whole range of seven main categories used to reflect topic areas.

The funding of research

The development of systematic funding is a good means of gauging the progress of any growing profession that relies on confidence and investment. The economic importance to the nation of studies in animal behaviour was much better acknowledged by the time the Second World War ended, and the expansion of various types of specially funded research areas after 1960 had been presaged by the growth of a significant range of financial sources assisting behavioural studies in the 1940s and

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[33]Bell, C.R. (1966) The future of psychology in British university education. *Bulletin of the British Psychological Society*, 19, 64: 7-12.
[34]Lowe, G. et al. (1977) Topic areas in psychology as represented in British university examinations. *Bulletin of the British Psychological Society*, 30: 218-9.

1950s. The papers surveyed in Appendix I acknowledge not just the authors' institutions' research funds and endowments, but also a selection of support from various sources, such as the Royal Society, Medical Research Council, Agricultural Research Council (who funded a number of Junior Research Scholarships), Department of Scientific and Industrial Research, Mental Health Research Fund, Nuffield Foundation, Ford Foundation, Carnegie Trust and Nature Conservancy. Commercial interest was also beginning to become more evident after the war, as in sponsorship by the Glaxo pharmaceutical company of M.R.A.Chance's work in 1946.[35]

James Drever[36] outlined the main sources of government income for financing psychological research by 1969.[37] These consisted of the University Grants Committee and the Science, Social Science and Medical Research Councils, administering £167 million (U.G.C.) and £30 million (Research Councils) to all departments that qualified for assistance. The Science Research Council limited itself to the biological and experimental parts of psychology, which might also receive help from the Medical Research Council. Sometimes, research in a university department might be directly commissioned by a government department, such as the Ministry of Defence. Research in clinical psychology was undertaken with funds from the Medical Research Council, National Health Service and, in the case of teaching hospitals, universities: these funds were administered by Regional Hospital Boards, individual hospitals and universities, or pooled under super-regional trusts. Drever pointed out that the allocation of resources for psychological research was haphazard and a matter of luck, but that the system, or lack of it, at least allowed for diversity. The Scientific Affairs Board of the British Psychological Society was perhaps worried by this lack of organization and planning of fund provision when it instigated an enquiry by M.P.Haggard and B.Shackel.[38] The Research Councils co-operated and a report was published in the *Bulletin of the British Psychological Society* in 1978. Support for psychological research by the Research Councils and also other sources of funding

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[35]Referred to in *Bulletin of Animal Behaviour*, no.6, January 1948.

[36](1969) Financing psychological research. *Supplement to the Bulletin of the British Psychological Society*, 22: 14-15.

[37]Reference is made to *Scientific research in British universities and colleges 1967-68*, then the latest in the annual series published for the Department of Education and Science and the British Council by HMSO. Volume II covered Biological Sciences (formerly Life Sciences). Sections were arranged in alphabetical order of university, listing the topics of research. In addition there were alphabetical lists of names of research workers and of the subject matter of the research, and addresses and telephone numbers of the institutions involved. The Research Councils themselves published annual *Handbooks* and *Reports*.

[38](1978) Monitoring financial support for psychological research. *Bulletin of the British Psychological Society*, 31: 3-8.

were investigated, and some details of the findings are given below. It was concluded that an attempt to streamline the process of funding by a more exact definition of the areas of interest of the Research Councils could lead to inflexibility, and less chance of funding enterprising research that did not fit a conventional mould and which reflected the interdisciplinary nature of much psychology-orientated work.

Support for psychological research was identified by dividing the subject matter of research into several headings, including ones for physiological and comparative research. It was noted that across areas the total Research Council funding pattern did not bear out the frequent assertion that psychology was preoccupied with animals. 'Much physiological work is concerned with human electrophysiology and, although physiological work was not subdivided according to species, even if 50 per cent were animal-based only 11 per cent of the total would be concerned with animals.' The level of support in thousands of pounds per annum for comparative and physiological research in psychology is given below,[39] in Table 1. To provide the details for Table 2,

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[39]Table 1 (1974)

(Key: a. Source and destination of funds.
b. Support in thousands of pounds per annum for comparative work.
c. Support in thousands of pounds per annum for physiological work.
d. Total support in thousands of pounds per annum for all types of research work.)

a	b	c	d
M.R.C.			
Psychology departments	4	36	258
Hospital and clinical departments (except psychiatry)	0	2	56
University non-clinical departments*	17	25	140
University psychiatry departments	3	19	127
Units**	0	75	751
Total	24	157	1332
S.S.R.C. total	0	0	204
S.R.C.			
Psychology departments	45	7	86
Hospitals	3	0	3
University non-clinical departments*	18	49	79
Psychiatry departments	0	0	2
Total	66	56	170
Grand total (£k)	90	213	1707

*Non-psychology, non-clinical departments cover a wide variety of pure, applied and social science subjects. Education is the most important.
**Units with 'psychiatry' in their titles are not included.

Table 2
Percentages of funds received by respondents to the Scientific Affairs Board Inquiry (S.A.B.I.). S.S.R.C. data from the S.S.R.C. figures, and percentages from Table 1, are included for comparison purposes. All percentages are rounded to the nearest half per cent.
(Key: a. Comparative, b. Physiological, c. Total amount.)

heads of departments of psychology were asked to identify all externally sponsored projects in psychology started between 1 August 1971 and 31 July 1974, and others started earlier and completed (as regards funding) between those dates. Of 71 departments of universities and polytechnics, 17 did not reply and 9 stated that they received no relevant funding. Although the response rate was good, some of those who did not respond were large departments probably receiving substantial grants.

A quantitative analysis of research work, 1960 - 1980

A detailed survey and analysis of all British work related to the study of animal behaviour as reported in four representative journals between 1960 and 1971 is given below in Appendices II and III. Appendix II reveals the varying levels of output of published papers from all of the research centres. Appendix III is geared to researchers with a high published output, and additional information is also supplied on their work bases (linked to dates of publication), fields of interest and experimental animals. Reliance on four journals for this survey is based on the same justification given for the use of a limited but representative number of journals for the survey of the preceeding period ending in 1959 (see above). However, it will be recalled that the role of the *British Journal of Psychology* in reporting work in animal behaviour was clearly declining, reflecting a trend that began as soon as the other three specialist publications cited here appeared after the Second World War.

The sources selected for the survey of this period make reference to 95 different research centres accommodating staff who published from them papers appearing in one or more of the journals. In these terms, the most productive sites were Madingley (48 out of 507 papers published overall), the Department of Psychology at Cambridge (32), Oxford's Institute of Experimental Psychology (28) and Department of Zoology (22), and the Agricultural Research Council's Poultry Research Centre, Edinburgh (22). Among the new universities, Sussex's School of Biological Sciences and Laboratory of Experimental Psychology soon began a tradition of high output in this

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	a	b	c
S.S.R.C. Inquiry	0	2.5	£2198k
S.S.R.C. (S.A.B.I.)	0	3.0	£723k
All government non-S.S.R.C. (S.A.B.I.)*	0	16.0	£2637k
Non-government (S.A.B.I.)**	0	14.0	£994k
* + **	0	15.0	£3631k
All Research Council from Table 1	5	12.5	--

period (17).[40] The position these sites occupied between 1960 and 1971 can be compared with similar data for the earlier and later periods in Appendix VII.[41]

The use of categories coded for cross-referencing is made in the presentation of a record of all British work (as published in any journal) reported in *Behavioural Biology Abstracts*, 1973[42] (Appendix IV) and *Animal Behaviour Abstracts*, 1980[43] (Appendix VI). The international coverage of journals by this series of abstracts was thorough,[44] and so a comprehensive explanation of the nature and extent of activity in the two sample years analysed (i.e. part-1972 to part-1973 and part-1979 to part-1980) is provided. Appendices IV and VI also contain tables showing the number of abstracts per author which appeared in the volumes of *Animal Behaviour Abstracts* of the period between the two sample years. From these details, and from a search for further authors unrepresented in Appendices IV and VI, another fully comprehensive survey is supplied for the intervening period, in Appendix V, of all workers in Britain producing at least ten articles for abstraction between 1972/3 and 1979/80 overall. The immense output of work in the 1970s has made it necessary to focus in this way only on those who published the most work as reflected by *Animal Behaviour Abstracts*, but this is considered to be an adequate as well as a practical representation of the pattern of research development in Britain. An explanation of the codes used is supplied in Appendix VII, and, in earlier appendices, details and notes are given on contents and arrangement.

An account is thereby given of animal work in the period from 1960 to 1980. The tabular layout of the information from the *Abstracts* also permits detailed comparisons between elements, as desired, and the formulation of, for example, percentages to reflect levels of output of centres and individuals, levels of use of types of animal, or

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[40]Appendix II, column f.
[41]Category 1, columns c to f.
[42]Bateson, P.P.G. et al. (eds) (1973) *Behavioural Biology Abstracts*. London: Information Retrieval Ltd.
[43]Bateson, P.P.G. et al. (eds) (1980) *Animal Behaviour Abstracts*. London: Information Retrieval Ltd.
[44]*Behavioural Biology Abstracts* vol.1, 1973, became, in later volumes consisting of quarterly parts, *Animal Behaviour Abstracts*, and from 1982 was published by Cambridge Scientific Abstracts. Approximately 5,000 international, primary journals and other source references were regularly monitored, to produce about 1,200 abstracts per quarterly issue. 'All journals specifically devoted to animal behaviour are monitored, as well as those publications in important fringe areas and those relating to the biology of particular taxonomic groups. Individual papers published in edited collections are included.' The Editorial Adviser was, from 1973, P.P.G.Bateson of the University of Cambridge. Much of the abstracted material emanated from the United States of America, but the British presence was substantial in view of the massive overall coverage (e.g. 1974, 300 out of 3849 abstracts, 7.77%; 1975, 389 out of 4198, 9.27%; 1976, 431 out of 4548, 9.48%).

levels of interest in particular subject areas. Categories used (and explained in Appendix VII) to describe types of animal or fields of interest are as compiled by the *Abstracts*: further refinement would be possible by reference to the original, individual abstract itself.

In the 1973 volume, 283 out of a total of 3,340 (8.47%) abstracts referred to papers describing work carried out in Britain; in the 1980 volume, the figures were 517 out of 5,838 (8.86%). The comparative totals in each of the four keyed categories of Appendix VII are provided so that differences in output, interest and use within and between 1973 and 1980 (as well as for the earlier 1938 - 1959 survey) can be identified: each element in each category has been totalled, using information from the tabulated record of the relevant contents of the volume of abstracts used. The fourth category permits an assessment of journal use.

Category 1 of Appendix VII is able to show the significant participation of departments of zoology in studies of animal behaviour throughout the period: it is interesting to note the frequency of their appearance as compared with that of departments of psychology. In Cambridge, it is possible to compare the outputs of the Psychological Laboratory, Sub-Department of Animal Behaviour, and Department of Zoology proper. The output of some centres (e.g. Anti-locust Research Centre, London, or Department of Psychology, Durham) declined in the mid-1960s, while at the same time others grew and flourished (note especially the Laboratory of Experimental Psychology at the University of Sussex and the Department of Psychology at the University of Hull). There is also much evidence that behavioural work undertaken to serve other subjects and disciplines increased in the 1970s, and among the highest levels of output the total number of individual author attributions per paper per site between 1973 and 1980 gives the Sussex departments 137; at Cambridge the Department of Experimental Psychology 110, Madingley 49, the M.R.C. Unit for the Development and Integration of Behaviour 43 and the Department of Anatomy 42; the Institute and Department of Experimental Psychology at Oxford 106; the A.R.C. Poultry Research Centre at Edinburgh 77; the Department of Psychology at Birmingham 74; and the Institute of Psychiatry at the Maudsley Hospital 54.

A brief inspection of Appendix V will reveal for the period 1973 - 1980 the most frequently recurring names, together with the associated sites, fields of interest and animals used. Some, like F.V.Smith of Durham, had been exceptionally productive in the 1960s, but are lost in these later tables. Others, like D.G.M.Wood-Gush or

D.I.Williams, continue to be prominent in 1973. A few, such as R.A.Hinde, appear at all stages of the survey, from 1952 to 1980. The tables of Appendices IV and VI allow partners in authorship to be linked, and the codes for cross-referencing may be used to establish details on a chosen individual or group and to establish links with others. For example, in 1973, the Department of Zoology at University College, Swansea was solely represented by P.F.Brain, who had three single-author papers abstracted. By 1980, he merited ten abstracts, some written with colleagues at Swansea, including, on one occasion, collaboration with the Department of Psychology. His papers appeared in ten different journals; he showed wide interests (physiological correlates, groups and social behaviour, chemical stimulation and drugs, aggression, dominance, communication and, especially, hormones); and his research animal was the rat. The favoured fields of interest among the whole experimenting community between 1973 and 1980 are shown in Appendix VII,[45] where they can be immediately be compared with those for the period before 1960.[46] Author attributions for the major areas of interest are as follows: chemical stimulation and drugs, 251; brain lesions, 132; sexual and reproductive behaviour, 117; hormones, 116; communication, 115; maintenance behaviour (foraging, ingestion etc.), 109; and ontogeny, 108. The first two of these areas of interest had been poorly represented before 1960. Throughout all periods, the rat and mouse have remained the most frequently used animals. Birds overtook insects for second place; and primates became regarded as increasingly important experimental subjects.[47]

Although all of the work analysed here was undertaken in Britain, some of it was carried out by foreign visitors. As far as has been possible, only experimental work has been included. Work that may have been theoretical reveals itself in an examination of the tables, but there is very little of it recorded here. In *Behaviour*, for example, the emphasis was on experimental papers, often written by foreign workers visiting Britain; or on papers originally submitted as Ph.D. theses and including much detail. Information on foreign visitors and on staff appointments was regularly reported in the final pages of issues of the *Bulletin of the British Psychological Society*.

The importance and influence of individual researchers can also be recognized from citation of works, information from (and to some extent length and replication of) obituaries, and from the frequency of general references. Prominent individuals are

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[45]Category 2, columns d, e and f.
[46]See column c.
[47]Appendix VII, Category 3, columns c, d, e and f.

chosen to review books, and have their books reviewed, on a regular basis. They may edit and contribute to books which become well used.

Using citation counts, a survey was published in 1977 to show the impact of departments of psychology and their staff.[48] The citation scores for each department were not sub-divided into subject areas, only a total all-encompassing figure being supplied to indicate comparative performance rates. However, although the same method was used to describe the relative impact of individuals, it is interesting to note the performance of those known to be particularly involved in animal work. Only those British psychologists listed in university calendars who held full faculty positions in university departments of psychology were included in the survey, otherwise John Bowlby, with 250 citations, and Donald Broadbent, with 242, would have been mentioned in the rank-ordered list of the '25 most cited psychologists in British departments of psychology according to the Social Science Citation Index'. This list was updated in a second article,[49] and details from both lists are supplied below.[50] Just as Broadbent and Bowlby had been omitted, so in the second survey, and for the same reasons, Richard Gregory at Bristol and Michael Shepherd of the Institute of Psychiatry were not included.

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[48]Rushton, J.P. and Endler, N.S. (1977) The scholarly impact and research productivity of departments of psychology in the U.K. *Bulletin of the British Psychological Society*, 30: 369-73.
[49]Rushton, J.P. et al. (1983) Research production and scholarly impact in British universities and departments of psychology: an update. *Bulletin of the British Psychological Society*, 36: 41-4.
[50]The most cited psychologists in British departments of psychology according to the 1975 S.S.C.I.: those involved in animal behaviour, with comparative rank order, university, and citations for 1975 (and 1974):

H.J.Eysenck	1st	London, Institute of Psychiatry	537	(628)
J.A.Gray	5th	Oxford	90	(99)
P.L.Broadhurst	6th	Birmingham	75	(37)
N.S.Sutherland	12th	Sussex (Experimental)	56	(106)
N.J.Mackintosh	14th	Sussex (Experimental)	54	(62)
M. Treisman	23rd	Oxford	41	(26)

Those making a contribution to British psychology (including animal behaviour) with more than 100 S.S.C.I. citations in both 1980 and 1981, showing comparative rank order:

			1980	1981
H.J.Eysenck	1st	London, Institute of Psychiatry	813	856
M.Rutter	2nd	London, Institute of Psychiatry	632	807
R.A.Hinde	8th	Cambridge, Sub-Department of Animal Behaviour	293	326
C.Blakemore	11th	Oxford, Department of Physiology	257	279
R.Dawkins	12th	Oxford, Department of Zoology	149	271
N.Tinbergen	15th	Retired, formerly Oxford, Department of Zoology	150	251
N.J.Mackintosh	24th	Cambridge, Department of Experimental Psychology	220	179
J.A.Gray	25th	Oxford, Department of Experimental Psychology	184	172

An obituary of K.R.L.Hall by R.C.Oldfield[51] explains that Hall's interest in animal behaviour developed strongly because of the opportunities available to him when the occupant of the chair of psychology at the University of Cape Town (1955 - 1959). In 1959 he succeeded G.C.Drew at Bristol, and the Department of Psychology there flourished as he continued to engage in personal research, setting about 'the task of raising the scope and scale of primatological studies in this country to the level they deserve and require ... he installed the facilities and resources needed to introduce - and persuade to breed - fresh primate species as experimental animals'. He arranged exchanges of research facilities for graduate students and other workers between Britain and a centre in Uganda, and took an active share in primate developments in the United States. 'Major plans for a substantial increase of research at Bristol were almost realized' but prejudiced by his death in 1965. 'The gap he leaves in contemporary British psychology is serious.' It is interesting to note that Hall had preserved a tradition of studies in animal behaviour at Bristol extending back to Lloyd Morgan's arrival as Professor of Geology and Zoology in 1883, a tradition interrupted only by the period between G.C.Grindley's final departure for the Cambridge Psychological Laboratory in 1933 and the arrival of his erstwhile pupil there, G.C.Drew, as Professor of the new Department of Psychology in 1951. Drew also provided an obituary for him in the *Bulletin of the British Psychological Society*, confirming that 'it was at Cape Town that he first became interested in the ethological and ecological studies of birds and primates for which he has since gained an international reputation'. At Bristol he achieved greatly improved accommodation.

> He believed wholeheartedly in the need to keep experimental, laboratory work and field observational work in intimate contact with one another. He combined in himself an unusual capacity in both areas. The new space enabled him to build up laboratory stocks of birds and primates on which he was working at the time of his death. His work rapidly attracted able young men, both psychologists and zoologists, to work with him. Many of them became involved in field work in Africa, as well as in the laboratory research ... Almost every conference on animal behaviour, wherever it was held, seemed to have a contribution from him.[52]

On Hall's death in 1965 he was succeeded by J.Brown, but John Crook took over avian and primate research direction, concentrating on social ethology, and focusing on the significance of social structures of species populations as adaptive and adaptable systems. Crook was interested in the dispersion of individuals in populations

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[51](1965) Obituary: K.R.L.Hall, 1917-1965. *Quarterly Journal of Experimental Psychology*, 17: 356.
[52](1966) Obituary: K.R.L.Hall. *Bulletin of the British Psychological Society*, 19, 62: 43-4.

in terms of the evolution of behavioural strategies that optimized the sometimes conflicting needs for both resource management and predation protection. As a student he had noticed the importance of the relationship for the foraging patterns of black-headed gulls of the diurnal rhythmicity of their dispersal system with the differing rhythmicity of the tide cycle, and the importance of the proximate factors relating ecology and behaviour within a system of demographic and social adaptability. Later, at Bristol, he studied such factors through behavioural and endocrinological experimentation with Quelea in the laboratory.[53]

News from the Cambridge Psychological Laboratory in 1968[54] recorded that in 1966 Dr Larry Weiskrantz had been appointed to a readership in physiological psychology in recognition of his outstanding work on brain mechanisms and behaviour in primates; but after only a year he was elected to the chair of psychology at Oxford, taking his erstwhile research assistant, Dr Alan Cowey, for five years a university demonstrator in Cambridge. Following these resignations, assistance in maintaining physiological psychology was provided by Dr G.Horn (Anatomy School), Dr L.L.Iversen (Pharmacology Department) and Dr L.J.Herberg (Institute of Neurology, Queen Square, London). Recent appointments to the research staff included Dr Susan D.Iversen as Senior Assistant in Research, Dr Joan G. Stevenson as a university demonstrator in experimental psychology, and M.J.Morgan as Assistant in Research.

Two years later, J.S.Huxley died. Although the bulk of his pioneering studies of bird behaviour had taken place before 1960, in 1965 he organized a Royal Society symposium on ritualization which resulted in a volume of the Royal Society *Transactions*, 'at the same time a testimonial for the fertility of his ideas and a challenge and a stimulus for further work.'[55]

Professor D.M.Vowles of Edinburgh died in 1985. He had been trained as a zoologist and was early influenced by Tinbergen and the Oxford ethology group. He later worked on the insect brain and as Senior Student at King's College, Cambridge, he developed precision methods for fine localization of electrodes in the ant brain. Following his appointment as Lecturer in Physiological Psychology at the Institute of Experimental Psychology at Oxford, he was later made Reader in 1964. At that time he began a programme to investigate the behaviour caused by brain stimulation in doves and to establish the hormonal control of reproduction in these birds. Assisted by

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[53]Crook, J.H. (1989) op. cit., pp.6 & 8.
[54]Zangwill, O.L. (1968) op. cit.
[55]Tinbergen, N. (1975) Obituary: J.S.Huxley, 1887-1975. *Animal Behaviour*, 23: 482-3.

his continued liaison with Tinbergen, his work was true neuroethology, combining very detailed analysis of courtship behaviour with physiology, as exemplified by his 1967 paper on the after-effects of brain stimulation in the ring dove, or that of 1970 on 'neuroethology, evolution and grammar'. Vowles became Acting Director of the Institute in 1965 and steered through plans for new buildings for both psychology and zoology at Oxford. Taking up the professorship in psychology at Edinburgh in 1968, he increased the research activities and encouraged interest in developmental psychology.[56]

A month after Vowles's, the death occurred of W.Sluckin. Between 1951 and 1960 he had worked with Professor F.V.Smith, Douglas Graham and Robert Thomson to develop a psychology department and degree at Durham. With his colleague Eric Salzen he began his major research into early learning and imprinting, many of his early papers establishing for himself a reputation as an experimentalist in animal behaviour. Joining the new department at Leicester in 1960, he remained there until his death. Research grants enabled him to begin extensive research, the production of some twenty papers, and books such as *Imprinting and early learning* (1964) and *Early learning in man and animals* (1970). He held visiting fellowships and professorships in the U.S.A., Canada and Australia, and received a personal chair at Leicester in 1965 before succeeding S.G.McK.Lee as head of the department in 1973. He published his last book, *Maternal bonding*, in collaboration with his wife and with his successor, Martin Herbert, in 1983.[57]

New theories, directions and achievements in the research activity of the 1960s and 1970s

The academic status and relations of comparative psychology

Many general and specialist articles have discussed or speculated on the progress of experimental psychology and related areas in the study of animal behaviour since 1960. Sometimes an historical perspective is introduced, while at other times the author attempts to lay emphasis on a proposed new definition for a particular trend in research, or even to question the validity of a whole area like comparative psychology,

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[56] Wright, P. (1985) Correspondence concerning D.M.Vowles. *Bulletin of the British Psychological Society*, 38: 232-3.
[57] Thomson, R. (1985) Obituary: W.Sluckin, 1919-1985. *Bulletin of the British Psychological Society*, 38: 234-5.

but a general feature of the period has been the renewed awareness among psychologists of the inter-relationship between psychology and philosophy. In the first half of the twentieth century, experimental psychologists were eager to continue with the task of separating their work from the charge of introspection and subjectivity and to establish a true independence for their subject. Many of them had enough background or knowledge in philosophy itself to be able to articulate this process. But since the mid twentieth century philosophy has re-emerged to question much of the content of psychology, and the psychologists are no longer equipped to answer back in what has appeared to be a battle for the mind. In 1944 R.G.Collingwood had described psychology as the fashionable scientific fraud of the age, and convincing philosophical objections continued, especially when psychologists took it upon themselves to examine thinking, motivation and personality.[58]

In 1960, R.C.Oldfield gave an address which reflected on the development of experimental psychology and considered its future.[59] He acknowledged that ethology had provided much information in a form which could be extended and refined by the use of physiological and pharmacological expedients, there being a need for direct checks by physiological observation. Oldfield believed that 'we are only at the beginning of what we can learn about ourselves by studying animals'.[60] He suggested that in psychological research it would be necessary to be quantitative; not to invent new descriptive terms and concepts more than was strictly necessary, as they were apt to get out of control; in pursuing experimental work to try to keep in as close touch with physiological and anatomical factors as possible; and not to neglect the opportunities offered by a systematic natural history approach, especially when strict experiment seemed to have come to a dead end. For the future, many new fields were opening up in which, especially in collaboration with physiologists, zoologists, pharmacologists, geneticists and engineers, the experimental psychologist could work with every prospect of being led to basic issues. He believed that the growth of psychology would be within the framework of the biological sciences: this meant striving to regard human behaviour as objectively as the biologist looks at the behaviour of animals. It was likely that psychology would be instrumental in extending the range of fundamental biological conceptions, although the usefulness and the limitations of work upon animals had become much more clearly appreciated. 'We no longer suppose that even careful controlled experiments on the abilities of rats to run

[58]Hearnshaw, L.S. (1987) *The shaping of modern psychology*. London: Routledge & Kegan Paul, pp.227-9.
[59]Oldfield, R.C. (1960) Experiment in psychology - a centenary and an outlook. *Advancement of Science*, 17: 364-74.
[60]ibid., p.371.

mazes after the removal of part of their brains is likely to make any particular contribution to the general problem of our own cerebral processes.'[61] Other lines of investigation would now benefit from technological advances that provided better instrumentation and precision, assisted by the increasing scale and freedom of collaboration between psychologists and those who worked in a great variety of other fields. Psychology, he said, could not stand by itself, and demanded, just as did other biological sciences, connection with and support from other disciplines. Accordingly, students should be given an opportunity of learning the elements of neighbouring scientific fields.

A year later, W.H.Thorpe[62] reviewed developments in the study of animal behaviour as witnessed by the recent literature. His article was entitled 'Comparative Psychology', but within it he explained the particular characteristics of ethology and the fruits of research in that field. Indeed, he suggested that 'we are all ethologists in the new sense' (of adopting objective, experimental approaches to problems), and that this regular chapter in the *Annual Review of Psychology* should be renamed 'Ethology'. Thorpe reviewed work in the analysis of instinctive behaviour, neurophysiology and drive in instinct, the analysis of releasers, orientation, rhythms of behaviour and in miscellaneous areas such as the investigation of exploratory behaviour, reinforcement, and developmental changes in learning capacity.

In an attack on behaviourism and an appreciation of the lasting value of the work of Hobhouse, L.S.Hearnshaw[63] commented that the previous twenty years had seen a revival of genuinely comparative studies and a breakdown of the conceptual straitjacket of reductionist behaviourism.[64] Ethology was throwing new light on the social behaviour of animals, and on phenomena such as circadian rhythms and periodicities. Gradually and inevitably, he said, this work had had an impact on psychologists. They had been forced to recognize that not all organisms were similar; that in fact each species presented its own behavioural problems and was a subject for

[61] ibid., p.373.
[62] (1961) Comparative psychology. *Annual Review of Psychology*, 12: 27-50.
[63] (1966) The comparative psychology of mental development. *L.T.Hobhouse Memorial Trust Lecture* no. 36, 5 May 1966, Bedford College, London. London: University of London, Athlone Press.
[64] P.L.Broadhurst, himself strongly influenced by American methods, expressed views the following year which went some way to echo this standpoint: 'What of the future? ... What is of paramount interest for the psychologist is the *interaction* of the environmental and genetical determinants. We seem to be emerging from a period in which a somewhat uncritical environmentalism prevailed, especially in American psychology, but let us not go too far in the opposite direction.' (1967, *Psychology in its natural habitat, an inaugural lecture delivered in the University of Birmingham on 16 February 1967*. University of Birmingham.)

study in its own right. There was, therefore, no simple overall formula which neatly fitted all forms of behaviour.

> The contrivances of organic life are richly diverse, and to cope with this diversity psychologists must diversify the species they study in their laboratories. Already there is no longer the old excessive concentration on a few docile species. Psychology departments are becoming very often miniature menageries, stocked with worms, insects, fishes, birds, and mammals of many kinds. Comparative psychology has indeed been reborn.[65]

While in Britain K.R.L.Hall was in the forefront of research on primates until his early death, the study of these animals having been one of the most stimulating developments since the end of the Second World War, the behavioural study of invertebrates was also proving rewarding, as when J.Z.Young and others[66] included in their research on the octopus, a suitable experimental preparation for their purposes, a detailed examination of the brain and nervous system, their chief interest. Young's studies had already yielded much information on the brain mechanisms involved in shape recognition, on the distribution of functions in the octopus brain, on the role of distance receptors and time delays in the evolution of cerebral complexity, etc.

> Even at the octopus level Young estimates that 90% of the cerebral neurons are concerned with decision-making - to attack or withdraw, food or danger. This is no simple stimulus-response mechanism but a system containing a complex hierarchy of levels, the teasing out of which demands combined behavioural and neurological analysis ... Plans, decision processes, images, thought, the self - and then consciousness. All the old bogies have returned from exorcism. Consciousness had to be brought back, partly because its physiological correlates were being laid bare and partly because of the functional importance of levels of consciousness in real-life situations.[67]

Hearnshaw also stated that it was necessary to re-assert psychology as the science of mind, because the psychologist should be concerned with the central structures and processes lying behind behaviour rather than with behaviour itself. Other concepts were also due for rehabilitation. Thorpe had accepted the general idea of purposiveness in behaviour, but many psychologists had resisted teleological concepts and purpose in the late 1950s and early 1960s. Of emergence, the Cambridge

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[65]ibid., pp. 13-14.
[66](1964) *A model of the brain.* Oxford: University Press.
[67]Hearnshaw, L.S. (1966) op. cit., pp.15 & 19.

psychologist Gregory[68] had described it as 'a doctrine of despair'. But, Hearnshaw said, 'Nature is not additive; when two things are put together in a meaningful way something new is generated which can no longer be described in terms of the qualities of the constituents ... development is not lawless or haphazard but subject to its own developmental laws.' He concluded: 'The central task of the psychologist is to investigate the evolution of mind. It is only against a background of developmental process that mind and its resultant behaviour can be explained.'[69]

D.Pritchatt[70] felt, too, that in the mid-1960s undergraduate teaching of comparative psychology should involve the forging of a link with the general field of biology so as to make it possible to lean on that discipline's own conceptual framework. The heterogeneity of psychology suggested interdisciplinary borrowing within a framework of evolutionary theory.

In a critical assessment of the state of contemporary psychology R.B.Joynson[71] warned of the dangers of exaggerated reliance on the validity of experimental results, and of the belief that psychology should be the study of behaviour rather than mind, as though accurate, objective and valuable data could then be expected. Humphrey and Summerfield were accused of over-confidence, while Zangwill was shown to have developed suitable caution. External and internal variables persistently threatened to deceive the experimenter: if they were not recognized or catered for (and this was extremely difficult), his results, thought to be valid, would in fact be false. Eysenck referred to this problem when rejecting S-R psychology,[72] and so did Broadbent,[73] although the latter appeared to want to try to develop behaviourism rather than abandon it. Individual differences in organisms also created variation in results.[74] Joynson[75] concluded that a direct physiological study of internal conditions was the only solution, but one yet to be made possible only when techniques and knowledge improved; thus, psychology would be distinguished from physiology only in so far as it concerned itself with the function of the whole animal rather than a part. However, Joynson saw little difference between psychology and neurophysiology, and

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[68]Gregory, R.L. (1961) The brain as an engineering problem. In: Thorpe, W.H. and Zangwill, O.L. (eds) (1961) *Current problems in animal behaviour*. Cambridge: University Press.
[69]Hearnshaw, L.S. (1966) op. cit., pp.22 & 23.
[70](1966) op. cit.
[71](1970) The breakdown of modern psychology. *Bulletin of the British Psychological Society*, 23: 261-9.
[72]Eysenck, H.J. (1965) *Fact and fiction in psychology*. London: Penguin Books, p.14.
[73]Broadbent, D.E. (1961) *Behaviour*. London: Eyre and Spottiswoode, p.132.
[74]Eysenck, H.J. (1966) Personality and experimental psychology. *Bulletin of the British Psychological Society*, 19, 62: 1-28.
[75](1970) op. cit.

Zangwill[76] believed that 'the neurology of today may well provide the psychology of tomorrow with its basic principles'. When this happened, said Joynson, psychology would cease to exist. 'The history of modern psychology is a record, not of scientific advance, but of intellectual retreat.'[77]

Two years later, in his Presidential Address to the British Psychological Society, Harry Kay expected substantial progress in biological psychology, but it is interesting to note that neurophysiological examples were given: the early attempts to unravel the memory coding of the neural system; the study of the interaction of the two hemispheres; and that of the necessary attributes of a visual analysing system. 'It is gratifying how much the laboratory facilities in this area have improved over the last 15 years in Britain.'[78]

The alleged decline in comparative psychology was addressed by J.Wilcock,[79] who proposed as an alternative the study of 'psychogenetics' to examine evolutionary adaptive processes among species, or behavioural evolution and phylogeny. L.Weiskrantz[80] also emphasized the importance to theoretical accounts of behavioural mechanisms of physiological findings in brain research, while recognizing the methodological difficulties. Furthermore, just as psychology should be dependent on physiological data, units of the nervous system were so numerous and capable of so many variations that unless it was known what the organism as a whole did behaviourally it would be very difficult to say how it was achieved physiologically or to plan selective physiological investigations. The practical results of work in this area included replacement therapy for Parkinson's disease, with L-dopa and dopamine, and substitution therapy. Weiskrantz also took the opportunity to point out that such results would be threatened by any research policy that sacrificed basic research for so-called applied research. A few years previously, P.L.Broadhurst had also mentioned the practical results of experimental learning theory for clinical psychology.[81]

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[76]Zangwill, O.L. (1964) Physiological and experimental psychology. In: Cohen, J. (ed.) (1964) *Readings in psychology*. London: Allen & Unwin, p.130.
[77](1970) op. cit., p.268.
[78]Kay, H. (1972) Psychology today and tomorrow. Presidential address to the British Psychological Society, Nottingham, 7 April 1972. *Bulletin of the British Psychological Society*, 25: 177-88.
[79](1972) Comparative psychology lives on under an assumed name - psychogenetics! *American Psychologist*, June: 531-8.
[80](1973) Problems and progress in physiological psychology. Based on the presidential address, Section J, British Association for the Advancement of Science, 6 September 1972. *British Journal of Psychology*, 64, 4: 511-20.
[81]'Clinical psychology is an area in which the notable advances of recent developments in the laboratory, especially those concerned with learning theory and, I might add, largely based on the outcome of animal experimentation, can fruitfully be applied to the alleviation of human suffering due to abnormal behaviour. This is particularly so in the treatment of well-defined neurotic symptoms

In an account of the 'state of the art' of psychological research published in 1979,[82] Iversen contributed a chapter on pharmacological studies in relation to disorders of mood and action, and discussed ways of identifying anti-anxiety drugs, the bases for congruent actions of different drugs and some ideas about the chemical basis of extreme moods, and Parkinsonism. Rolls dealt with the effects of electrical stimulation of the brain on behaviour: in particular, reinforcement effects were tied in with variations in hunger and thirst and with relevant aspects of psychopharmacology. In the same year, the relation between behaviour and chemical factors became the subject of another survey.[83] British contributors included Smart on the effects of undernutrition on brain development and behaviour, Cooper on behavioural studies of drug interactions (- one of the few detailed accounts then available in this field), and Crow and Deakin on the possible neurochemical bases of the psychoses (a rapidly moving field) and of consciousness. The reviewer confirmed that the book covered several areas in which progress was rapid, although very little progress had been made in the field of drug effects on learning and memory. A group of three chapters provided an account of the factors controlling food and water intake, covering metabolic factors in the control of feeding (Booth), interactions between feeding and drinking (Toates) and the pharmacology of food and water intake (Blundell and Latham). These three chapters, said a reviewer,[84] nicely illustrated the advances made in the field through the convergence of contributions from many different ones: 'The days of studying limited aspects of behaviour following non-specific electrolytic lesions are, happily, long past'. Another group of three chapters dealt with maternal, sexual, aggressive and fear-motivated behaviours. These behaviours were not discussed in isolation from each other, but the material was grouped around the effects of hormones of the pituitary-gonadal and pituitary-adrenal axes (Brain) and the inter-relationships between fear, pain and aggression (Rodgers). The chapter on chemical communication between animals (Brown) concentrated on rodent behaviour and discussed the sources of chemical signals, their perception and their influence on social behaviour: apart from the products of special scent glands, rodents also produced volatile substances in their urine and faeces that could influence the behaviour of other animals. The nature of these substances was influenced by diet, hormones and the animal's emotional response.

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as they affect behaviour, and it is fitting that the first venture of the new Department into graduate course work should be into this area and this in turn will encourage research, both comparative and human.' Broadhurst, P.L. (1967) op. cit., pp.23-4.

[82]Connolly, K.J. (ed.) (1979) *Psychology survey no.2.* London: Allen & Unwin.

[83]Brown, K. and Cooper, S.J. (eds) (1979) *Chemical influences on behaviour.* London: Academic Press.

[84]File, S. (1979) *British Journal of Psychology*, 72: 521-2.

Two books expressed a range of views held by prominent British researchers in animal behaviour as they had developed by the 1980s. *Exploration in animals and humans*, edited by J.Archer and L.I.A.Birke,[85] updated earlier investigations made in the 1950s and 1960s by D.E.Berlyne. Chapters by Russell and Cowan reflected the recent development of behavioural ecology, with its emphasis on the functional or cost-benefit analysis of behaviour. Stevenson, Wood-Gush and others dealt with environmental influences and abnormal behaviour in captive, wild and domestic animals respectively, reflecting the comparative approach to behaviour. Russell reviewed earlier theories of exploration and discussed possible current explanations, while the associated research work of Cowan and Barnett was described. Morris discussed the effect of brain lesions in rats on exploratory activity, while Einon and Hughes dealt with play in relation to exploration, and Sluckin with novelty. Another book, *Animal intelligence*, edited by L.Weiskrantz,[86] was an assessment of past and contemporary attempts to rank the intelligence of different taxa. MacPhail concluded that the best hypothesis was that there were no differences in intelligence at least within higher vertebrates, ability differences only being caused by advantageous 'devices' like human language. But Mackintosh demonstrated that there were quantitative differences in the speed of solution of problems: the comparisons of closely related species, such as pigeons and jackdaws, were considered more productive than similar earlier tests of fish, birds and mammals. With Mackintosh, Dickinson believed that animals may possess and use explicit knowledge of the consequences of their actions, even following instrumental conditioning. Gaffan and Passingham were both concerned with differences in the ability to use contextual cues in order to decide which learned strategy to follow.

<u>The realignment and internationalization of comparative psychology, ethology and sociobiology, and their effects on perceptions of the man-animal relationship</u>

To mark his retirement, a book of essays was published in 1975 that reflected the influence and importance of Niko Tinbergen in the development of ethology.[87] Tinbergen[88] had characterized ethology as the biological study of behaviour involving

[85]Gaffan, E.A. (1984) Book review: Exploration in animals and humans by Archer, J. and Birke, L.I.A. (eds) (1983) Wokingham: Van Nostrand Reinhold. *British Journal of Psychology*, 75: 290-2.
[86]Andrew, R.J. (1985) Book review. Animal intelligence by Weiskrantz, L. (1985) Oxford: Clarendon Press. *British Journal of Psychology*, 76: 553-4.
[87]Baerends, G. et al. (eds) (1975) *Function and evolution in behaviour: essays in honour of Professor Niko Tinbergen, F.R.S.* Oxford: Clarendon Press.
[88]Tinbergen, N. (1963a) On the aims and methods of ethology. *Zeitschrift fuer Tierpsychologie*, 20: 410-33.

four classes of question, on the causation, ontogeny, survival value and evolution of behaviour. Many of the studies that he instigated at Oxford were continuations of those with which he had been involved at Leiden. For example, stickleback studies were carried on by Desmond Morris, Fae Hall, Beatrice Tugendhat, and others, right up to the work of David Wilz in the late 1960s. Tinbergen, with his associates and students, concentrated especially on the behaviour of black-headed gulls, using comparative observation combined with experimental approaches. They began in this area of study with an investigation of the causal basis and functional significance of egg-shell carrying, and continued with an examination of other apparently anti-predator features in the reproductive behaviour of the gulls, including the spacing of the nests and the timing of the cycle. Functional questions such as these, and their bearings upon questions about the evolution of behaviour, had been at the heart of Tinbergen's ethology during his time at Oxford. Furthermore, his popular books, films (such as 'Signals for Survival') and talks on radio and television brought ethology and animal behaviour study to the general public. In 1973, he shared the Nobel Prize for Medicine with Lorenz and von Frisch.

Another commemorative publication appeared the following year.[89] It contained the proceedings of a conference held in 1975 to mark the 25th anniversary of the founding of the Sub-Department of Animal Behaviour at Madingley. Entitled *Growing points in ethology* it was divided into four sections on motivation and perception, function and evolution, development, and human social relationships. Peter Medawar mentioned the freshness and spontaneity of ethology which other biologists found so enviable, but the editors concluded with a suggestion that the increasing wealth of evidence should be marshalled by some degree of formalization. The reviewer[90] commented that there was still a great deal of conceptual confusion in the behavioural sciences and in ethology itself. In the section on motivation Richard Dawkins discussed hierarchical organization: the working out of this concept in behaviour studies was likely to be uncovering the basic property of living things as manifest in their behaviour. D.J.McFarland and J.C.Fentress discussed the organization of behaviour in terms of form, function and interactional processes, McFarland concentrating on cost functions of behaviour and 'pay-offs', Fentress on the ability of factors to activate more than one class of behaviour under certain circumstances. R.Andrew discussed attentional processes; Peter Marler, social organization, communication and graded signals; B.C.R.Bertram, kin selection; T.H.Clutton-Brock and P.H.Harvey, primate social

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[89]Bateson, P.P.G. and Hinde, R.A. (eds) (1976) *Growing points in ethology*. London: Cambridge University Press.
[90]M.R.A.Chance (1976) in *British Journal of Psychology*, 69: 526-8.

behaviour and structures; and A.Manning, the place of genetics in the study of behaviour.

At the end of the 1970s, P.J.B.Slater expressed concern that there was a growing divide between two schools of ethologists, one considering the causes of behaviour, the other considering its function. As a neuroscience, ethology by then had diversified enough to encompass the work of biochemists, sociobiologists, behavioural ecologists, etc. 'Today most prefer to think in terms of individual behaviour patterns, each affected to varying degrees by a variety of internal and external causal factors. Rules which can be generalized across species or across behaviour patterns have proved hard to come by.'[91] The pursuit of the study of causes had resulted in more laboratory work: although there was the disadvantage of unnatural environments, research which could not be carried out in the field (such as physiological experiment) was possible in the laboratory, which also permitted of sophisticated quantification. With the abandonment of trust in explanations of causes by such concepts as 'instinct' or 'displacement activity', the area of causation of behaviour lacked the unifying theory it once had. But students of functional behaviour enjoyed the support of Darwinian theory, updated by the exciting advances in evolution theory achieved very recently.[92] However, they did not have the tools available to those studying causes in the laboratory. The different methods and problems of examining cause and function in this way became apparent. Slater did point out that in one area at least, in studies of foraging, theory and data had fortunately managed to keep pace with one another. He did not agree with E.O.Wilson that ethology was likely to be torn in half and consumed by physiology and sociobiology, because some preferred to study both cause and function, which were in any case sometimes very closely linked. Practical applications like livestock welfare and management proved its value and ensured a demand for it. Slater believed that the recent vogue for concentrating on how natural selection had shaped behaviour would be short-lived: 'The traditional subject matter of ethology - the study of mechanisms with an eye to their role in the natural life of the animal - has all the signs of greater staying power.'

V.C.Wynne-Edwards[93] had refocussed attention on the complexity of co-operative behaviour in animals and on the problems of interpreting it in terms of the selfish maximization of individual reproductive advantages. British workers had failed to see the great significance of William Hamilton's critical examination and solution of this

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[91]Slater, P.J.B. (1979) The two sides of ethology. *Trends in neuroscience*, February: 33-5.
[92]Dawkins, R. (1976) *The selfish gene*. Oxford: University Press.
[93](1962) *Animal dispersion*. Edinburgh: Oliver & Boyd.

problem in the context of the social organization of bees[94] for 'inclusive' fitness, but E.O.Wilson realized its sociobiological significance in supplying the basis for a neo-Darwinian account of general biological altruism, in which by kin selection assistance from one relative to another would be beneficial in terms of 'inclusive' fitness to the donor. John Maynard-Smith[95] also proposed the idea of the evolutionarily stable strategy of mating and parental behaviour, which must be linked to ecological influences such as food availability, and to possible reciprocal altruism or 'cheating' between pairs. But a problem that had remained was the difficulty of modelling, which itself became inadequate as the complexity of socioecological systems was shown in field study.[96]

Concepts such as altruism, co-operation and cheating in animal behaviour began to give some studies of it the characteristics of precise economic analyses in terms of investment, return and cost-benefit for individual and group behaviours. Such mathematical precision allowed sophisticated behavioural forecasts to be made, and computer modelling responded to these possibilities, as in the elucidation of fighting strategies by the use of the mathematics of 'Game Theory' by John Maynard-Smith at Sussex University.[97]

As ethology became firmly established in the British academic environment after the Second World War, reflecting the importation and acceptance of the theories and research methodologies of the continental ethologists, the position of laboratory-based comparative psychology began to weaken. Meanwhile animal psychology, as a discipline whose role was developing into that of studying processes useful to other disciplines such as pharmacology, psychiatry or agriculture meant that it became predominantly a secondary science, or even an applied technique, serving primary research programmes of other fields. In this way, the appearance of ethology helped to restore attention to those Darwinian and evolutionary theories which had been neglected after the turn of the century. The laboratory-based comparative psychology which had flourished in the USA and which had encouraged this neglect, being centred rather on the elucidation of principles affecting short-term observable learning behaviour under various artificial environmental conditions, has remained secure across the Atlantic, where it became a point of resistance to rival ethological interpretations. In the UK the laboratory after the Second World War was used for

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[94]Hamilton, W.D. (1964) The genetical evolution of social behaviour, I and II. *Journal of Theoretical Biology*, 7: 1-52.
[95](1972) *On evolution*. Edinburgh: University Press.
[96]Crook, J.H. (1989) op. cit., pp.9-15.
[97]Sparks, J. (1982) op. cit., p.276.

applied animal psychology rather than for that American style comparative psychology which had never in any case been fully accepted as an adequate substitute in Great Britain for evolution-based research. The arguments between the comparative psychologists and the ethologists in the USA reverberated in Britain, where ethological field studies became preferred as a means for examining animal behaviour as a primary research activity. Tinbergen's presence in Oxford from 1949 inevitably helped to foster this favoured scientific culture of animal behaviour studies. As ethological principles duly gathered strength in the USA, a rapprochement took place between ethology and comparative psychology, and in Britain the willingness of those such as Tinbergen to recognize and use laboratory-based methods meant that laboratory work in the study of animal behaviour in Britain reappeared after the Second World War in a new and invigorated form by courtesy of ethology.

By the 1970s the internationalization at least between continental Europe, the UK and the USA of the various forms of field and laboratory studies of animal behaviour was complete, achieved through a new level of publications, communications, conferences, collaboration, visits, residencies and exchanges. Such internationalization included western, westernized and developed, democratic countries, and in common with other pure and applied sciences and with the environmental issues often related to them, the subject, typically from the late 1960s onwards, was regarded by the research workers of the relevant nations now as a global one. Individual scientists from these nations might contribute now to an international discipline, not one linked to or dependent on the domestic conditions of a particular nation. The sharing of the Nobel prize in 1973 by Tinbergen, Lorenz and von Frisch demonstrated the transnational status of this and other scientific areas.

Just as the historical study of investigations of animal behaviour could proceed from an internal account of the achievements of the discipline to an examination of other external encouragements and constraints bearing upon it in the context of a domestic society, so the process of internationalization could now be extended from the domestic context to one where the universal and shared efforts of scientists gave the subject a new stimulus which reduced many external cultural factors and which would encourage once more simplified 'internal' assessments. When E.O.Wilson's *Sociobiology* was published in 1975[98] to offer new theories to develop ethology, which by then was a universal discipline equally identified with the laboratory as with the field, reactions to it were therefore given by an international readership concerned

[98]Wilson, E.O. (1975) *Sociobiology: the new synthesis.* Cambridge, Mass.: Harvard University Press.

with an international subject. The concept of cultural barriers did not play a part in the assessment of his theories. If there were in the post-war years any cultural barriers, they had been those erected within the scientific community itself, as originally by the rival comparative psychologists and ethologists, and they were not related to natural cultural predispositions or to political influences in the nations qualifying as described above for inclusion in the new internationalized scientific community.

The decade of the 1970s was therefore significant in a number of ways in the evolving pattern of encouragements and constraints of experimental animal behaviour studies in the UK, and it marked the end of a clearly identified developmental period. British workers, as others, contributed to a subject that was evolving at an international level. The award of the Nobel prize to Tinbergen[99] and his foreign colleagues was an outstanding demonstration of this new global environment for the science, as well as of the recognition of ethology (in field and laboratory form) as a truly significant international science, implicitly therefore eclipsing and overtaking traditional comparative psychology and animal psychology as pure research disciplines. It was to be within the ethological framework that further major theoretical advances would be made, and these could encompass international studies of animal behaviour in the laborarory and the field, drawing on the advancing information from the neurosciences, biochemistry and genetics as required. It was in these circumstances in the 1970s that sociobiology and concepts such as biological altruism and inclusive fitness in animal communities came fully to absorb the attention of the international scientific community and to re-establish the role of evolution in the interpretation of behaviour by extending and modifying Darwin's theories: the unit of evolution in studies of social behaviour was now not the individual organism, but the gene.[100] Hamilton's theory of kin selection to explain apparent altruism and provide for 'inclusive fitness' within the centripetal behaviour of a 'selfish herd' had been

[99] 'Nikolaas Tinbergen received the Nobel for his studies of animal behaviour, in acknowledgement of the importance of ethological research to the understanding of human behaviour. Best known for his studies of the habits of gulls, Tinbergen also researched the homing instincts of digger wasps, the mating rituals of sticklebacks, and the colour adaptations of butterflies. His later studies of autism in children were also noteworthy.' *The Who's Who of Nobel Prize Winners.* 2nd ed.

[100] In his Foreword to Konrad Lorenz's *On Aggression* (1963, translated by Marjorie Latzke, reprinted 1972, London: Methuen), Julian Huxley referred to Lorenz's interpretation of vertebrate behaviour as composed of 'behaviour units' (just as anatomy is composed of structural units), having a genetic basis and having through evolution become modified by Darwinian natural selection to act as specific signals for communicating emotional states, and having also become ritualized or formalized, with exaggeration of prominent features of physical appearance and with enhanced variety and signalling efficiency in behaviour patterns, some resulting in 'displacement activities' when there are conflicting drives.

presented in 1964, and in 1976 Dawkins proposed the 'selfish gene' as responsible for promoting inclusive fitness in groups of relatives within an evolving species.

Hamilton, a theoretical population geneticist rather than a functional biologist, provided a genetical mathematical model for interactions between relatives on one another's fitness that led to 'inclusive [Darwinian] fitness' resulting from a limited restraint on selfish competitive behaviour and from the possibility of limited self-sacrifices, such as caused by genetically transmitted qualities and benefits of parental care and full- and half-sib relationships. Biological principles for discriminate social evolution required that the positive selection of genes should result not only from increasing the fitness of the host, but also from increasing that of relatives, through behavioural transmission; or 'The social behaviour of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbours' fitness against his own according to the coefficients of relationship appropriate to that situation'.[101] Hamilton's study of group selection theory led to the topic of kin selection, concerning which Darwin[102] had formerly introduced the idea of natural selection operating at the level of the family rather than of the single organism, with special reference to the position of the worker castes of insect societies when it is the capacity to generate sterile but altruistic relatives that becomes subject to genetic evolution. Wilson[103] acknowledged that 'The modern genetic theory of altruism, selfishness, and spite was launched by W.D.Hamilton in a series of important articles [from 1964]. Hamilton's pivotal concept is *inclusive fitness*'. Looking to the future, Wilson stated that 'The transition from purely phenomenological to fundamental theory in sociology must await a full, neuronal explanation of the human brain ... Having cannibalized psychology, the new neurobiology will yield an enduring set of first principles for sociology'.[104] Evolutionary sociobiology would provide the background of historic adaptive development, and would monitor the genetic basis of social behaviour. In 1971 Wilson[105] had argued that when the same parameters and quantitative theory are used to analyze both termite colonies and troops of rhesus macaques, a unified science of sociobiology would result, and that:

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[101]Hamilton, W.D. (1964) op. cit.
[102](1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
[103]op. cit., p.118.
[104]op. cit., p.575.
[105]Wilson, E.O. (1971) *The Insect Societies*. Cambridge, Massachusetts. The Belknap Press of Harvard University Press, pp.458 & 460.

> ... the principal goal of a general theory of sociobiology should be an ability to predict features of social organization from a knowledge of ... population parameters combined with information on the behavioural constraints imposed by the genetic constitution of the species. It will be a chief task of evolutionary ecology, in turn, to derive the population parameters from a knowledge of the evolutionary history of the species and of the environment in which the most recent portion of that history has unfolded. This [is a] sequential relation between evolutionary studies, ecology, and sociobiology.

Because of the comparability of insect societies with vertebrate and human ones, 'sociobiology can eventually be derived from the first principles of population and behavioral biology and developed into a single, mature science'.

A further characteristic of the 1970s was the renewed interest in a particular form of the man-animal relationship. This interest involved both scientist and the public, in the UK especially at this time and abroad, and involved moral and philosophical considerations which were reminiscent of those expressed in the second half of the nineteenth century against a background of Darwinian theory that linked species and encouraged some to question the moral as opposed to the scientific justification of (then only physiological) experimentation on non-human animals. The renewed evolutionary emphasis of animal behaviour studies of the 1970s coincided with a revival of interest in moral aspects of the man-animal relationship.[106]

In British psychology and ethology, concern about this relationship and the role in it of the concept of ethical cost as incurred by various levels of experimental psychological intervention was set in motion in 1975, significantly the date of publication of *Sociobiology*, a work to which, as in the case of Darwin, reference was often made when attempts were undertaken to emphasize kinship and responsibility between man and animals. In that year, a long series of correspondence began in the *Bulletin of the British Psychological Society*, at first based around the thoughts of Richard Ryder and the high profile given to the issue of ethically unacceptable research in his *Victims of Science*. Within the next eleven years, the British Psychological Society, the Association for the Study of Animal Behaviour and the Experimental Psychology Society all recognized the need to formally acknowledge and regulate ethical cost,[107]

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[106]e.g. Clark, S.R.L. (1977) *The moral status of animals*. Oxford: Clarendon Press; Singer, P. (1975 and 1976) *Animal liberation*. New York Review and London: Jonathan Cape; Ryder, R.D. (1975 and 1983) *Victims of science. The use of animals in research*. London: Davis-Poynter Ltd and National Anti-Vivisection Society Ltd.

[107](1985) Guidelines for the use of animals in research. *Bulletin of the British Psychological Society*, 38: 289-91; (1981) Guidelines for the use of animals in research. *Animal Behaviour*, 29: 1-2;

in part stimulated by their own members and in part in reaction to much external pressure targeted on experimental animal behaviour studies that was growing in the late 1970s and beginning to influence public opinion to the extent that laboratory studies of animal behaviour might be threatened legislatively if not occasionally physically by the extreme element of the campaigners who had read and absorbed the animal rights literature of the anti-speciesist moral philosophers and who were successfully putting animal rights issues related to experimentation into politics once more. This political strategy also resulted in acceptance by the end of the decade that the 1876 Cruelty to Animals Act was due for early replacement, and this came about later in 1986.

(1986) Guidelines for the use of animals in research. *Animal Behaviour*, 34: 315-8; and (1986) Guidelines for the use of animals in research. *Quarterly Journal of Experimental Psychology*, 38B: 111-6.

CHAPTER 7

THE EXPERIMENTAL ANIMALS: FACTORS AFFECTING THEIR USE

Practical and methodological considerations

The practical limitations and advantages of using animals (in their own right or as opposed to 'human animals') for psychological and behavioural research have frequently been acknowledged and discussed since at least the turn of the century.[1] Such discussions were at first centred on the fundamental, theory-dependent question of the legitimacy of comparability which Darwin inaugurated; and then, once this legitimacy had won ground, on the more routine matters of procedural value and reliability in experiment. (Ethical considerations arose later as a consequence of the acceptance of legitimacy of comparability, a consequence with, therefore, a scientific basis rather than one resulting only from philosophical arguments, or from emotive and subjective traditions of common-sense morality. These considerations are considered separately, below.)

Following L.T.Hobhouse's popular description of his experimental work in *The Pilot*,[2] an article appeared in the same journal by Father P.N.Waggett SSJE who wrote that Hobhouse had rightly been unwilling to motivate his animals through real hunger to display their full capacities, and that experiments such as his therefore could not be as realistic as the influences experienced in the natural environment. Waggett also noted the resulting artificiality, and the effects of boredom, that must be encountered in using captive zoo animals: the chimpanzee performed well because of a dread of boredom and being ignored. The academic tests involved in psychological research spared the animals the urgency of fear or fighting (through being eaten or through competition) as found in the natural environment, and which sharpened their wits.

> Might it not be better to collect news of rogue elephants; to live almost within reach of savage dogs and observe their skill in nearing one's calves; to watch the procedure of crib-biters, runaways, buck-jumpers,

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[1]For example, John Lubbock (1915) in *Ants, Bees, and Wasps: A Record of Observations on the Habits of the Social Hymenoptera* (17th edition, London: Kegan Paul and Co.) reported: 'I originally intended to make my experiment principally with bees, but soon found that ants were on the whole more suitable for my purpose. In the first place, ants are much less excitable, they are less liable to accidents, and from the absence of wings are more easy to keep under continuous observation'.
[2]Hobhouse, L.T. (1902) The Diversions of a Psychologist. In: Lathbury, D.C. (ed.) (1902) *The Pilot (A Weekly Review of Politics, Literature, and Learning)*, vol.5, January - June. London.

> and other beasts in whom the primitive force of fear and hatred is unhappily strong ... something is lacking in the high, kindly, protecting experiments of deliberate research ... for the making of an animal 'senior wrangler,' to be a good animal crammer, perhaps a harder tone is needed,

as found in drivers, keepers and trainers (but not in such as Hobhouse, who had written in a rather sentimental way in these popular articles in *The Pilot*), who could provide harsher stimuli and work with animals more at their own level. 'The experiments, while so much removed in respect of *conditions* from the ordinary problems of animal life, are not sufficiently removed in *character*. They are the kind of thing that natural selection may deal with but here removed from the pressure of struggle.'[3] For example, the use of mild hunger as a stimulus in experiment was a poor substitute for the more natural and effective stimulus of real hunger as experienced in the natural environment; instead it might be better and more profitable in the artificial and relatively humane experimental situation to settle for unusual investigations which were themselves concerned with unnatural and artificial occurences such as the performance of tricks or the behaviour of the 'singing' dog. Otherwise, Waggett's views suggested a choice for the sake of truer understanding between observations of the later ethological type or those dependent on greater experimental harshness as accepted and employed by Thorndike and his other American contemporaries. Douglas Spalding had originally recognized the need to maintain as much of a natural environment as possible in order to elicit reliable information from his experimental subjects, and so in studying the comparative roles of instinct and learning in neonatal birds he built a box with a wire net front to it near the original nest before transferring the hatchlings. This enabled their confinement for study, but, at the same time, continued and uninterrupted feeding by their parents.

At the turn of the century, apart from laboratory studies of discrimination, learning or motivation by non-invasive observation, the major experimental techniques available for the study of brain function were ablation and electrical stimulation. The experimental convenience of the chosen animal was inevitably of great importance in laboratory work, and led to a preference for the rat . In the field, the question of convenience also became important. In 1934 observations of a herd of Scottish Red Deer benefited from the size and visibility of these animals which lived above ground,

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[3]Waggett, P.N. (1902) Article. In: Lathbury, D.C. (ed.) (1902) *The Pilot (A Weekly Review of Politics, Literature, and Learning)*, vol.6, July - December. London.

were sensitive to changes in the environment, had a well-developed community life, and for which a year formed a definite unit of time in their social lives.[4]

There have been distinct general practical advantages in the use of animals as opposed to human beings in experiments concerning the motivation of behaviour, whether laboratory investigation involving artificial, contrived motivation, or that kind which (as in field observation) does not. Animals have also been preferable in studies of instinctive behaviour, since it is often assumed that there is comparatively little unadulterated instinctive behaviour left in man, whose behaviour is frequently learned rather than inherited, and therefore less susceptible to an examination of genetic evolution within strains of the same species. Furthermore, it would be impracticable to consider selective mating in humans to achieve pure strains for the sake of such studies, both for ethical reasons and because of their slow reproductive rate; and the close control of the immediate conditioning environment necessary for this type of behavioural study could only be considered for animal work, again both for ethical reasons and because of the protracted human developmental period.[5] In learning and motivation experiments, human subjects are more likely than animals to vary their interpretation or treatment of the stimulus and of their behaviour subsequent to its effect.[6] But, although convenient to manage and manipulate, the behaviour of a given selected strain of, for example, the domesticated laboratory rat cannot be regarded as typical of general animal behaviour or indeed of rat behaviour. Preoccupation with laboratory studies has also limited the understanding of animal behaviour by researchers themselves. Deutsch, for example, admitted to his own surprise at discovering the natural burrowing behaviour of the rat in its natural environment outside the laboratory.[7]

The choice of experimental animals for use in behavioural studies in the laboratory has come to be governed by certain factors including availability; cost of acquisition; ease of accommodation, feeding, breeding and maintenance; prolificness; 'temperament', docility and tolerance of their own kind housed with them; robustness or susceptibility to illness; size and ease of handling or manipulation; refinement of strain; average life-span; and, of course, suitability for the given experimental project planned (often measured by adaptability and inquisitiveness). The psychological make-up of the

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[4]British Association for the Advancement of Science *Reports*, Sectional Transactions.-D., p.324.
[5]Broadhurst, P.L. (1963a) *The Science of Animal Behaviour*. Harmondsworth, Middlesex: Penguin Books Ltd.
[6]Watson, A. (1963) Learning. In: Humphrey, G. (ed.) (1963) *Psychology through Experiment*. London: Methuen.
[7]Deutsch, J.A. (1963) Experiments on animals. In: Humphrey, G., ibid.

animal must render it tolerant of captivity; its special living conditions should be readily reproducible; it must be resistant to infection; the fastidiousness of many wild animals in their choice of mate should be recognized; and, especially where isolation is necessary, the possibility and effect of pining or boredom must be assessed.[8] For all of the above reasons, the rat has proved a favourite choice throughout this century. References to reports of significant difficulties experienced by some of the earlier, less prepared British investigators have been made above.[9] The more recent frequency with which particular types of animal were used can be deduced under general headings from the information supplied below, in the appendices, and reflect the development of professionalism in psychology as species were matched accurately with experimental purposes and procedures.

D.Pritchatt[10] referred to the advantages of certain types of animal for undergraduate comparative psychology. In operant conditioning at Leeds, mice were found to be more suitable than rats because they were easier to handle and required less space. Pigeons were also used, and because of their visual acuity lent themselves particularly well to discrimination and stimulus generalization. He added: 'At present [in 1966], attempts are being made to enlist the aid of more primitive vertebrates like frog, water turtle (easily obtained and maintained during the summer) and fish, thus completing our behaviour sampling from all five vertebrate groups.' Invertebrates were also recommended, since they could be used to compromise between field studies and laboratory experiments of a somewhat artificial nature, it being a simple matter to set up micro-habitats. Pritchatt agreed with Pollard and Lysons[11] that animal studies enabled training in the techniques of experimental design: 'experiments with invertebrates, particularly, are often very cheap to run as well as making available a large number of subjects which enables the use of chi-square without the difficulties of

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[8]Rewell, R.E. (1957) The choice of the experimental animal. In: Worden, A.N. and Lane-Petter, W. (eds) (1957) *The UFAW handbook on the care and management of laboratory animals.* 2nd ed. Potter's Bar: Universities Federation for Animal Welfare, p.166ff.

[9]e.g. Flugel, J.C. (1954) A hundred years or so of psychology at University College, London. *Bulletin of the British Psychological Society*, 23: p.24; Smith, E.M. (1912) Some observations concerning colour vision in dogs. *British Journal of Psychology*, V, 2: 119ff; Macgregor, M. and Schinz, J. (1915) A study of learning and relearning in mice and rats. In: Edgell, B. et al. (1915) *Psychological studies from the psychological laboratory, Bedford College for Women, University of London.* London: Hodder and Stoughton; Hazlitt, V. (1917-1919) The acquisition of motor habits. *British Journal of Psychology*, IX: 299ff; Grindley, G.C. (1927a) The neural basis of purposive activity. *British Journal of Psychology*, XVIII: 168-88.

[10](1966) Comparative psychology as an undergraduate practical course. *Bulletin of the British Psychological Society*, 19, 65: 25-7.

[11]Pollard, J.S. and Lysons, A.M. (1966) A laboratory course in invertebrate behaviour. *Bulletin of the British Psychological Society*, 19: 31-3.

related samples readings ... biochemical studies can also be carried out (the effects of thyroxin on metabolic activities of tadpoles makes a useful experiment)'.

Similar practical considerations applied to work at a more elevated level. In describing the work of the Animal Behaviour Research Group at Oxford, Tinbergen stated:

> We should attempt to be economical with our resources, such as space and money - this is one of the reasons why part of our work is done with small animals which can be cheaply kept in the lab. (such as sticklebacks and Drosophila), and part with animals which Nature provides for us in the field (colonial sea birds). These considerations determined the character of the research programme, which consequently is a compromise between broadness of approach and penetration in depth.[12]

H.J.Eysenck and P.L.Broadhurst,[13] as behavioural psychogeneticists, described a detailed and practical aspect of the advantages of using strains of rats selectively bred for their behavioural characteristics in their Maudsley experiments: 'Defecation has been widely used as an expression of emotional responsiveness in small rodents, and there is a good deal of evidence for the validity of this measure.' Broadhurst also noted that 'Defecation is a response which does not present the usual difficulty encountered in behavioural work: it comes self-quantified, you might almost say, since the scores literally have to be picked up and disposed of.'[14]

The laboratory environment and its effect on distorting the natural behaviour of the experimental animal was assessed by M.R.A.Chance and J.H.Mackintosh.[15] The cage, as the normal means of accommodation between and during experiments, was the subject of their article, and was seen to affect the animal in a variety of ways. The effects could be general, affecting all captive animals, or specific to certain types of cage, or even to certain types of cage under particular experimental conditions. The effect could reveal itself as a general change in the animal's behaviour or as a specific change in a behavioural, physiological or pharmacological response. The sources of these effects might include the reduction of space, boredom through lack of diversity

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[12]Tinbergen, N. (1963b) The work of the Animal Behaviour Research Group in the Department of Zoology, University of Oxford. *Animal Behaviour*, XI: 206.
[13]Eysenck, H.J. (ed.) (1964) *Experiments in motivation*. Oxford: Pergamon Press, p.286.
[14]Broadhurst, P.L. (1967) *Psychology in its Natural Habitat. An Inaugural Lecture delivered in the University of Birmingham on 16 February 1967*. University of Birmingham.
[15](1962) The effects of caging. In: *Laboratory Animals Centre Collected Papers, report of a symposium held at the Royal Veterinary Laboratory on 11 April 1962, The environment of laboratory animals*. Carshalton: Laboratory Animals Centre, Medical Research Council Laboratories, pp.59-64.

in the surroundings or frustration through the same causes. For animals like mice, a 'retreat' was often necessary to prevent distress caused by other animals close-by or by noise, etc. Such a retreat could be formed from a simple division or covering placed in the cage. Isolation and strangeness might also affect the animal. Caging limits the company an animal may keep, and the group size that is selected by the experimenter could have a profound effect on the animals as shown by their reaction to various physiological and pharmacological tests. Mice in strange cages produce wet faeces, whereas those which have become habituated to their surroundings produce dry ones. A similar effect is caused by different numbers per cage, animals from large groups tending to have wet faeces and animals kept in fives having dry ones. The combination of habituation and territoriality is related to the 'home cage effect' by which there is a tendency for animals in their own cages to have the best of any encounters.

P.L.Broadhurst[16], in discussing the use of the rat and mouse in behavioural studies, concentrated on his own interest in psychogenetics. The widespread use of the rat in various studies could be explained by historical reasons. It had served the purposes of American psychologists, being well adapted in its natural habitat for running narrow enclosed pathways, and consequently suited to the study of learned responses to stimuli by means of the use of the maze. When this type of investigation developed in Britain, the same animal was favoured, and even though by the early 1960s other methods of investigation had to some extent displaced reliance on the maze as the instrument of choice, the rats remained in force. Because so much had been learnt about the rat over the course of the century, it seemed difficult to discard it, although many researchers, especially ethologists, were recommending the diversification of species interests as well as of the kinds of behaviour studied. Broadhurst stated:[17] 'Emphasis on learning alone, that is, on one aspect of the environmental determinants of behaviour, to the neglect of genetic variables as well as other influential background variables, often environmental but liable to interact with the genetic ones in affecting behaviour, and this emphasis limited to results from one species alone, created a climate inimical to the study of psychogenetics which is only now being eroded'. This situation had implications for two problems in psychogenetics, the evolution of behaviour and the creation of special strains by selective breeding. The most fruitful approach to the study of behavioural evolution was through the comparison of genetic determinants of behaviour in several species or sub-species simultaneously. The rat did

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[16](1963b) The choice of animal for behaviour studies. In: *Laboratory Animals Centre Collected Papers, report of a symposium held at the Royal Veterinary Laboratory on 29 May 1963, The choice of the experimental animal.* Carshalton: Laboratory Animals Centre, Medical Research Council Laboratories, pp. 65-80.
[17]ibid., p.69.

not represent a good starting point, because of the low number of inbred strains for analytical crossing. Many more such strains were available for the mouse. But for the creation of special strains by selective breeding, the rat was to be preferred, especially in view of the tried and tested methods available for measuring aspects of its behaviour. Broadhurst refers to his own development of the Maudsley Emotionally Reactive and Non-reactive Strains, using the open-field test. He adds that such selection almost invariably involves changes in characteristics in the organism other than those deliberately selected for, and these may surface in, for example, pharmacological tests. The Maudsley rats are considered as a convenient animal analogue, for heuristic purposes, of the fundamental personality dimension of neuroticism as defined and measured in humans. Broadhurst[18] says the question to ask now is not 'Which species or sub-species is best?' but 'Do there already exist strains of a suitable species applicable to the behavioural trait to be examined?' If the answer is 'no', strains should be selected using psychogenetic selection: 'the vision I am striving to conjure up is that of the behavioural scientist in the comparative field being able to construct his experimental population in advance'. Some thought is also given to the possible introduction of new species into the laboratory: there seemed a need for 'a mammalian species in which the genetic control of members of the same litter is absolute and comes together with a reasonable guarantee of uniformity of intra-uterine environment'.[19] He suggests the nine-banded armadillo, which invariably produces like-sexed quadruplets derived from a single ovum, and which could therefore throw light on the relative influence of common heredity and diversified environment. However, the animal's poor thermoregulation would make it an expensive laboratory tool, requiring special heating conditions or extensive facilities for a semi-natural type of environment. If these requirements were met, the effects of temperature variation on nest building or maze-learning (as a burrowing animal) could be studied.

R.J.Brittain and P.S.J.Spencer[20] further considered the choice of animals for pharmacological research, which frequently included studies of the effects of drugs on behaviour. Many pharmacological tests were based on either the potentiation or antagonism of effects induced by electrical, auditory, mechanical, thermalgesic or chemical means in laboratory animals. The authors stated that observational techniques using intact unanaesthetized animals were becoming increasingly important,

[18]ibid., p.73.
[19]ibid., p.75.
[20](1963) Factors governing the choice of animal species for pharmacological investigations. In: *Laboratory Animals Centre Collected Papers, report of a symposium held at the Royal Veterinary Laboratory on 29 May 1963, The choice of the experimental animal.* Carshalton: Laboratory Animals Centre, Medical Research Council Laboratories, pp.81-96.

particularly in view of the evaluation of potential psychopharmacologically active drugs by their effects on animal behaviour. The animals used should be healthy, disease-free and resistant to infection, and breed well; economy was also a factor. The animal most suited to the bulk of experiments was the mouse, followed by the rat. An animal's age and life-span had also to be taken into account, and related to the length of the test. Apart, too, from the consideration of size, the sex to be used had to be decided on. For example, induced fighting behaviour in mice, or the study of the effects of drugs on locomotor activity in rats, required the use of females for best results. The rat was well suited for the trainability required in avoidance, respondent and free-operant conditioning; and the squirrel monkey could be used to advantage for operant behavioural tests. This monkey shared the advantages offered by the rat, but could be used in more refined and elaborate tests. Other animals which could readily adapt themselves to changes of environment included the rabbit and dog. Finally, caution was needed in taking into account the widely differing susceptibility of animal strains to drug-induced effects, and many workers had drawn attention to the difference in the characteristics and reactions of animal species due to genetic variables.

Automation in the management of animals during maintenance and experiment began to attract more attention in the 1950s.[21] The rapid developments in animal studies at the University of Sussex in the 1960s were reflected in the sophistication of laboratory provision for behavioural work there at the end of the decade. A description was given of a system for running operant experiments using on-line control by computer in carefully designed facilities at the Laboratory of Experimental Psychology.[22] The emphasis of this article was on the equipment rather than on the animals. The chambers used needed to provide easy access; the opportunity for the experimenter to see the subject without himself being seen; a sound-proofed environment; economical construction; durability; and the saving of space. The solution arrived at by the authors allowed them to run simultaneously 49 animals in a room measuring 22 by 15 feet which also contained most of the programming equipment. Cubicles were of various sizes and stacked, and air-conditioning was incorporated. Data output occurred on-line through a teletype, or on a visual display (relayed by closed-circuit television to the animal running room), or on paper tape. Improvements were being made that

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[21]e.g. Wasservogel, E. and Hurwitz, H.M.B. (1958) An automatic feeding battery for small animals. *Animal Behaviour*, 6: 112-3.
[22]Sutherland, N.S. et al. (1969) A system for running operant experiments. *Bulletin of the British Psychological Society*, 22: 297-8.

would allow up to 40 animals to be run simultaneously on ten different experimental programmes running concurrently.

Encouragements and constraints occasioned by the recognition of ethical cost

The development and implementation of legal provisions

Between 1876 and 1986, apart from general laws designed to protect animals from mistreatment by the public at large, the main source of legal influence on the work of students of animal behaviour has been the Cruelty to Animals Act of 1876. The Act at first reflected society's concern to regulate physiological experiments in the light especially of reports of severely invasive research on the continent in the nineteenth century. Soon after the passage of the Act, the Association for the Advancement of Medicine by Research was founded by James Paget and others, and, at least until 1912, it vetted all licence applications for medical research before forwarding them to the Home Office Inspectorate, and offered support for its members in the face of antivivisectionist opposition. The Research Defence Society was formed in 1908 by Stephen Paget (son of James and secretary of the Association), with a similar role but one with an enhanced educational purpose. By 1980 charitable status had been achieved for this educational part of its activity. These organizations have represented the views of the experimenting scientific community in Britain throughout this century.[23] With the advent of laboratory-based psychological experimentation on animals, the 1876 Act was assumed to extend to this new area of activity, although its provisions did not appear to respond exactly to the implications of some work involving psychological stress, since it was designed to regulate vivisection rather than experimentation, and no psychological work was mentioned in the annual reports of the Home Office Inspectorate before the Second World War.[24] However, the Act has

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[23]Their representation was active at the time of the Royal Commission on Vivisection (1906-1912), the Protection of Animals Act of 1911, the Dogs Protection Bills of 1913 and 1927-1936, the Report of the Departmental Committee on Experiments on Animals (the Littlewood Committee Report on the Workings of the Cruelty to Animals Act) of 1965, the several Bills to amend the Cruelty to Animals Act in the 1970s, and the Animals (Scientific Procedures) Act of 1986. During this time no psychologists had ever been officers of the organizations.

[24]The attachment of the special Certificate A to a Licence, enabling experiment without anaesthetic, required that 'no operative procedure more severe than superficial venesection or simple inoculation may be adopted in any of the said experiments', but, taken literally, this would place no restriction on stressful psychological procedures. Furthermore, the Act stipulated that 'if an animal appears to an Inspector to be suffering considerable pain, and if such Inspector directs such animal to be destroyed, it shall forthwith be painlessly killed': an equivalence of pain and suffering through mental stress was not addressed.

been considered appropriate by most psychologists and its requirements were usually respected by them even if an argument might otherwise have been constructed to claim that a proposed piece of work fell outwith those requirements. Accordingly, psychologists have worked within the spirit of the Act and have recognized specific advice given in recent decades by the Research Defence Society in its *Notes on the Law Relating to Experiments on Animals in Great Britain (The Act of 1876)*, first published in 1950. This was reprinted in 1967 and 1969, and then superseded by *Guidance Notes on the Law Relating to Experiments on Animals* which was itself cooperatively based on guidance notes compiled by the Inspectorate and, until publication by the Society in 1972 and in subsequent editions, had not been generally available.[25]

The application of the Act to psychological work was therefore based on consideration of two elements which could be applied commonly (but with varying degrees of exactness) to a broad range of work in any of the experimental sciences involving living vertebrate animals: 'experiments' (procedures for which the outcome is not known in advance) 'calculated to cause pain' (if likely to interfere with an animal's health, comfort or integrity). As a result, some mild psychological experiments where no aversive stimuli were used, such as the motivation by food reward of rats to learn mazes, of the kind used at Bedford College for Women before the First World War, would not require a licence. But if the same experiment had been calculated to cause pain, perhaps by the use of severe food deprivation or punishment by electric shock, it would become licensable. Much therefore depended on judgements made by psychologists when designing an experiment about whether it fell within the Act and

[25]The edition of 1974 advised that 'Procedures calculated to cause stress, including those designed specifically for behaviour studies require specific authority ... Conditioning by reward alone would not require the authority of the Act ... Intention to affect any of the special senses by damage or deprivation requires a detailed description and explanatory notes ... [For Certificate A work without anaesthetic, including] Exposure to sensory stimuli such as mild electric shock ... [state] intensity, duration, frequency, period of administration, and whether the animal is to have the facility of avoidance or not ... [An experiment within the meaning of the Act] must be calculated to give pain; the Home Office interpretation of this phrase is made in the widest sense as including the possibility of discomfort, distress, disease, or other disturbances of normal physical or mental health, [i.e.] any procedure which may interfere with the normal well-being of a vertebrate animal other than killing, if it be done for the purpose of experiment'. Students were advised that 'Procedures that may cause undue fear, fright or stress would be considered as calculated to cause pain. Examples of these procedures would be very loud noises, very bright lights, and the conditioning experiments such as Pavlov did where the reinforcement is painful'. It was acknoweldged in the *Guidance Notes* of 1974 that 'There has not been sufficient specific research into housing, lighting, nutrition, genetics, husbandry practices, and diseases of laboratory animals, with the result that there is as yet no consensus of opinion amongst the major users in this country as to what the ideal conditions should be in detail'. Research Defence Society (1974) *Guidance Notes on the Law Relating to Experiments on Animals*. London: Research Defence Society.

required description, submission, approval and a licence.[26] In the process of making such decisions, during the earlier years of the Act, it is probable that neither the psychologist nor the Home Office would have taken into account other factors related to but not part of the experiment itself, such as the suitability of accommodation and its effect (perhaps highly distressing but not 'causing pain') on the animals used. Some of these factors, often dependent themselves on the development of scientific knowledge, have come to have equal status in animal welfare issues, and are better addressed in later legislation.[27] Another deficiency in the 1876 Act - a reflection on its original focus on physiology - was the standard requirement for anaesthesia followed by destruction during an invasive experiment. Some psychological experiments do not involve surgery but can be classified as 'calculated to cause pain' (as in electric shock), and for obvious reasons, require conscious animals, most of which will undergo repeat or long-term investigations: while licensable, these experiments have not therefore carried the usual anaesthesia and destruction condition, but have been covered by the award of a supplementary certificate accounting for their special requirements. In much psychological work, the animal remains fully healthy or makes a complete recovery, and this has led also to the argument, for reasons of economy in experiment, for the use of the same animal in further research.

The 1876 Cruelty to Animals Act has always been regarded as a compromise, as has its successor, reflecting the pressures of those have advocated as well as of those who have opposed the experimentation. According to one side, the Act has been a constraining influence, limiting the range of psychological work and disbarring work that is readily undertaken in countries such as the U.S.A.: most British psychologists

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[26]Blackman, D.E. (1981) Regulating psychological experimentation with animals in the United Kingdom. *Psychopharmacology Bulletin*, vol.17, no.2, April, p.85, comments: 'In practice ... psychologists in Britain who use animal subjects have come to be regarded as operating within the Act, and they invariably hold a licence and appropriate certificate ... Within the British tradition of legal constraints, a system has evolved by custom and precedent. This is founded on open and informed discussions between experimental psychologists and the Home Office Inspectorate, and it has made it possible for psychological research with animals in the U.K. to be both scrutinized and protected.' But Ryder, R.D. (1983) *Victims of science. The use of animals in research.* London: Davis-Poynter Ltd and National Anti-Vivisection Society Ltd, p.53, refers to morally questionable maternal deprivation experiments with monkeys at the Medical Research Council's Unit at the Sub-Department of Animal Behaviour in Cambridge (described in *Animal Behaviour*, vol.19, 1971) which had not been licensed because the Home Office had considered them as being outside the Act.
[27]Blackman (op. cit., p.87) notes that 'psychologists have long recognized that the experience of pain is both difficult to judge and dependent on the general circumstances in which a noxious stimulus may be presented. Similarly, psychologists are accustomed to evaluating the possible disruptive effects on psychological and behavioural well-being of environmental circumstances which do not necessarily give rise to pain as such. In short, psychologists should generally be more alert than some other scientists to the subtleties of how animals interact with their environmental circumstances, and are therefore in a position to heighten awareness of the possible impact of all experimental procedures.'

have accepted the need for this constraint, but a few have complained at the practical limitations resulting in their research plans, and one or two have appeared to have deliberately ignored the requirements of the legislation. According to the other side, whose belief is equally true, the Act has enabled, through the issuing of licences and certificates, work to be carried out with the protection of the law which would in other circumstances and under other existing laws have been open to prosecution by the State or individuals. It was in these other circumstances that Robert Prescott of St Andrews University was successfully charged by the Scottish Society for the Prevention of Cruelty to Animals under the Protection of Animals (Scotland) Act 1912 of experimental ill-treatment, since he was not protected by the 1876 Act. He had been supervising a postgraduate in the study of feline predation behaviour in artificial laboratory conditions, where a variety of prey was 'ill-treated, tortured or terrified'. At the trial, Home Office Inspectors (who had visited the experimental site but were unaware of this particular procedure) asserted that they would not have granted a licence if an application had been made, and R.A.Hinde as expert witness confirmed that the experiments were cruel. Prescott's licence for other work was then revoked, although he denied any cruel intent and relied on the argument of increasing scientific knowledge.[28]

In many ways the Act has been seen as an unsatisfactory compromise by those opposing experimentation, but as a necessary price to pay for the protection of their interests by those in the laboratory dependent on, as well as subject to, its legal sanctions. Blackman[29] asks whether any legal system of constraints encourages moral awareness: perhaps, on the contrary, it tempts the scientist to attribute the business of ethical assessment to the establishment alone. He feels that just as ethical decisions concerning human subjects are centred on the professional judgement of psychologists, so, too, should those concerning animals remain 'internal' to psychology. However, this proposal must be unsatisfactory, since humans are comprehensively protected by a variety of laws, and no enabling law exists to allow comparable human experimentation. Animal experimentation is enabled as much as restrained by the Acts related to it, because without the protection of the current Act in force, experimenters could be prosecuted under other laws against cruelty. Furthermore, possible or actual levels of concern about ethical cost have frequently been governed and influenced by the type of psychology absorbing an individual or a scientific community at a given time. This has been the case with Behaviourism, which minimized subjective and

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[28]Hollands, C. (1989) Trivial and questionable research on animals. In: Langley, G. (ed.) (1989) *Animal experimentation - the consensus changes*. Basingstoke: Macmillan Press, pp.120-3.
[29](1981) op. cit., p.88.

unquantifiable elements such as pain and emotional experience, and attacked any kind of anthropomorphism and encouraged a Cartesian attitude to animals as organisms without claims on our rational feelings (as revealed by its 'value-free' working terminology and vocabulary, involving the use of such reductive words as 'vocalization'). In the U.S.A., and, when imported, in the U.K., such psychologies would serve to reinforce an exclusive laboratory ethic which could hardly be expected to meet the standards of consistent and representative ethical questioning which Blackman was ready to assign as the responsibility of the psychological profession.

Critics of the Act have often questioned its efficacy 'on the ground', noting especially the limited number of Inspectors. In 1885, c.800 experiments were licensed, by 1895, 4,679, and by 1905 this number had risen to c.38,000, leading to the Second Royal Commission in 1906, not just because of the increase but also because most experiments by that time were being carried out without anaesthesia. The Commissions then began to examine 'experiments, whether by vivisection or otherwise'. Approximately one million experiments took place in 1939, and by 1963 this number had further grown to c.4.2 million. Because of the latter increase, the Littlewood Committee was constituted to report on the adequacy of the administration of the 1876 Act.[30] Other critics have complained at the absence of prosecutions under the Act as indicative of its ineffectiveness (although this could also suggest the reverse, resulting from widespread compliance). It is therefore important to look for evidence of the process of decision-making and enforcement necessary to a convincing implementation of the Act's provisions.

The nature of psychological experiments and their relative infrequency, especially before the Second World War, have resulted in a limited appearance in the official records of the Home Office, whose Advisory Committee on the Administration of the Cruelty to Animals Act 1876[31] was charged with the duty of monitoring implementation, relying on the specialist opinions and evidence of the Inspectors in the field, and subject to the authority and ratification of the Home Secretary. An inspection of these records of reports of cases requiring its special attention, which are housed in the Public Record Office, gives an impression of a high level of consistent

[30]Written evidence was given by the Association for the Study of Animal Behaviour, and oral evidence by O.L.Zangwill, concerning the examination of pain in animals, but there was no participation by the British Psychological Society or the Experimental Psychology Society, and no reference to psychological experiment in the text, either concerning discussion of the range of work or of public opinion. *Report of the Departmental Committee on Experiments on Animals (Chairman Sir Sydney Littlewood)* April 1965. Cmnd. 2641. London: HMSO.
[31]Since 1980 this has been the Advisory Committee on Animal Experiments.

attentiveness and objectivity exercised by the Committee, which over the decades (between the 1920s and 1960s at least), gave no sign, in its documentation or deliberations of psychological work, of being a cat's-paw of the scientific establishment, in spite of a membership which was science-oriented.[32] The level of rigour with which the Committee dealt with applications for licences for psychological work, or the monitoring of them, is revealed by a number of examples in Home Office records.

In 1921, F.A.E.Crew,[33] Director of the Animal Breeding Research Department at the University of Edinburgh, who was interested in heredity and addressed the British Association for the Advancement of Science on it, had his licence suspended for allowing an assistant to do his licensable work for him. The work involved the removal, implantation and transplantation of glands and gonads, and the administration of gland extracts to examine sex ratios and development. It was agreed by the Committee not to renew his licence in 1922; nor at this time was he given full support in his application by his head of department.[34] The Home Office referred to Crew's 'false and disingenuous statements' in this matter, making him 'unfit to hold a licence', while recognizing the effect this might have on his career. In 1926-7, Crew was in trouble again for exceeding the limits on numbers of animals and frequency of experiments as set out in his licence. The Principal of Edinburgh University was informed by the Secretary of State of the Home Office of a reprimand given to Crew: his behaviour was considered 'particularly serious because he holds a responsible position as head of a laboratory'. Following a warning from the university, and an abject apology, he was later awarded a licence once more.[35] By 1939 he had become professor in the university's Institute of Animal Genetics, and in 1940 he was elected a Fellow of the Royal Society.

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[32]This science orientation did not encompass psychological science until in the 1950s professors of psychiatry or psychological medicine became eligible to act as signatories in support of applications for licences under the Act (PRO HO 285/15).

[33]Crew has been mentioned above as one who, like Victoria Hazlitt of Bedford College for Women, attempted to question William McDougall's Lamarckian experimental findings.

[34]Professor Sir Edward Sharpey Schafer F.R.S. The reason not to give this support was based on Crew's physical and organizational separation from the work in question, but it was stated that Crew would be recommended for dismissal if in future he did not adhere to the Act in letter and spirit - an example perhaps of an institution at least embarrassed and eager to retain the privileges accorded by the licensing of its laboratories.

[35]PRO HO 45/24715. The Department of Animal Genetics was opened in 1930 and Crew and Sharpey Schafer corresponded at the time on the problem of antivivisection opposition, Sharpey Schafer asserting at the opening ceremony that all medical advances were based on animal experimentation. WIHM CMAC PP/ESS E. 3/1-12.

A number of applications for licences and certificates for behaviour-related studies which were submitted in the early 1950s attracted more special attention from the Advisory Committee.[36] The records include details given by scientists who had reported as required, having completed licensed or certificated work. These included, for example, A.L.Walpole and J.M.Ledingham who had carried out a programme of rat parabiosis. Ledingham reported in 1950 that the series of experiments 'has been extremely valuable in elucidating the problem of experimental hypertension'. A full and representative record of the process of submission, approval and report-back is provided by the work of Dennis H.Chitty between 1950 and 1955, when the Advisory Committee described his work with J.R.Clarke as 'psychological experiments with voles'. On 31 July 1950 Chitty, a biologist and Deputy Director of the Bureau of Animal Population, applied for a licence to experiment at the Oxford University Science Buildings in Banbury Road. As required under the Act he described the nature of the proposed experiments: 'To keep voles under conditions likely to result in fighting for the establishment of a social hierarchy' and to carry out 'A study of the physiological mechanisms involved in population control by intraspecific competition'. He was also required by the Act to 'State how the experiments are designed to advance by new discovery physiological knowledge or knowledge useful for saving or prolonging life or alleviating suffering', to which he responded by explaining that his work would examine the 'effect of social stress upon longetivity and reproduction with particular reference to the adaptation syndrome (Selye)'. Chitty believed that the mechanism through which normal functions are impaired might be that of Selye's adaptation syndrome, and if so, there would be changes in the adrenal, thymus and other endocrine glands of animals subjected to the stress of fighting.[37] An Inspector, Dr P.L.C.Carrier, commented on the application: 'The experiments proposed are unusual if not novel, and though no actual operative procedures by the licensees themselves are involved, the animals concerned in the experiments will be deliberately exposed for varying periods to severe injury which must in many cases be fatal.' J.R.Clarke (an Australian Rhodes Scholar) provided the Committee with the necessary report on the outcome of their experiments. 'These experiments have demonstrated, for the first time, the existence of natural stressing agents - chasing and fighting - in

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[36]PRO HO 285/13.

[37]Both Chitty and Selye (as well as Noble and Collip, see below) were Canadians who shared an interest in studies of stress and means of experimentally producing it. Selye published widely on stress and his work, which was particularly criticized by antivivisectionists, led to the identification of a stressed-induced hormone which was later reproduced synthetically for use in medication (ACTH and Cortisone). Chitty (and Zuckerman, see below) would have worked in Britain in circumstances under which the law and the Advisory Committee would apply greater restrictions than those experienced in the prosecution of this sort of work by their Canadian-based counterparts.

natural populations. The work has implications for a very large field of endocrinology and pathology.'[38]

An application for a licence and certificate to carry out another 'stress' experiment, from A.A.Mikhail, was refused by the Advisory Committee on 3 July 1963.[39] He described the proposed experiments with rats to restrict access to food, except for a minimum period of four hours, in any period not exceeding 44 hours, over a maximum period of 20 days; to restrict animals' movement by constraint for a single period of not longer than 48 hours; and to administer electric shocks to the feet of up to a maximum intensity of 2.0 milliamperes, of a maximum duration of 10 seconds with a maximum frequency of 400 per day over a maximum period of 20 days. The object of the experiments was 'to elucidate the mechanisms by which emotional factors affect the development of gastric lesions'. 'The Committee were unanimous in regarding the experiment as crude in conception and inexcusably severe in terms of pain. They strongly recommended that it should not be allowed.' Such refusals were not resticted to the less established workers. An application by Zuckerman to study the behavioural effects of the amputation of the forelimbs in rodents was similarly rejected.

The Home Office was also approached for advice on how domestic legislation might be extended in special situations to regulate the work of those not operating within the usual British scientific environment. One such situation arose in the Second World War, upon the arrival of American forces in Britain. In June 1941, the American Red Cross-Harvard Field Hospital Unit, based in Salisbury, applied successfully for registration as a laboratory where animal experiments could be done. In 1942 the Unit became the responsibilty of the U.S.Army Medical Corps, which at first requested freedom from U.K. domestic law in this area of activity as in others, but appropriate discussions and arrangements were effected from 1943. These arrangements were confirmed in 1945 also for educational work with frogs, rabbits and turtles at the U.S.Army's Shrivenham American University.[40] In 1952, following these similar arrangements between the Home Office and the U.S.Army Medical Corps,

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[38]Clarke continued in more detail: 'Natural populations of voles possibly consist of a number of individuals lacking organization. They are populations of strangers. From the first experiment mentioned above, data have been obtained from:- i The efficacy of strangeness in making voles fight ii The factors which influence success in fighting iii The development of fighting behaviour from juveniles to adults iv The effect of fighting on the growth of the combatants. These four items are important to any theory of population dynamics. It has become clear that fighting in voles is probably determined by:- i Genetic factors ii Humoral factors. This is again important to theories of vole population dynamics.'

[39]PRO HO 285/79.

[40]PRO HO 45/25087.

promulgated in 1943 under wartime conditions, an agreement was drawn up between the Home Office and the U.S.Air Force concerning regulation, licensing and certification of experiments, all of which would be carried out at 32 Grosvenor Square, London, by the staff of the 494th Clinical Laboratory Unit, although other hospital laboratories might use frogs for pregnancy tests. Under this agreement, the U.S.Air Force would use the British regulatory system and enforce it itself, via its own Inspector.[41]

Shortly after the Second World War, on 2 November 1946, a letter was sent by the War Office to the Home Secretary seeking confirmation that no licence was needed for the War Dogs Training School of the British Army of the Rhine, where Royal Army Veterinary Corps officers were designing experiments on dogs trained in mine detection in which the olfactory nerves would be cut and other operations carried out in order to determine how the dogs detected mines. The response of the Home Office was to indicate that the experiments could proceed because they were to take place abroad, but that if the work had been proposed for the U.K. a licence might well have been refused. The Home Office also noted that if the work in Germany was made known in Britain, there could be a public outcry, and it would then be up to the Secretary of State for War to provide an explanation.[42]

The psychologist's viewpoint

There are very few published references belonging before the 1970s to the viewpoints of psychologists concerning those ethical questions which are today raised in connection with behavioural research on animals. Because of his contribution to psychology and his understanding of the principle of mental continuity between man and animals, it might be expected that Darwin himself would have held and expressed influential opinions, but these were necessarily (for historical reasons) restricted to issues surrounding physiological work, and although he explained a personal revulsion to the unnecessary infliction of pain and could not contemplate carrying out experiments personally, he felt vivisection to be necessary to advance knowledge. T.H.Huxley's standpoint was very similar,[43] and so too was that of Romanes.[44] In the

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[41]PRO HO 285/83.

[42]PRO HO 45/25867.

[43]But Alfred Russell Wallace's was not; and he suspected that much cruelty served the wish of scientists to improve careers and reputations (Ryder, R.D., 1989, *Animal revolution. Changing attitudes towards speciesism.* Oxford: Basil Blackwell, p.160). Huxley himself expressed abhorrence to Darwin over the self-confessed indifference to animal suffering of a scientist (Dr Emanuel Klein, a

time of Darwin and Huxley, however, it was still considered no shame at least to acknowledge and regret, as they did, the cost in terms of experimental suffering occasioned to further the ends of science. After the turn of the century, many behavioural scientists indeed began to regard such reservations as unnecessary, and also shameful to the extent that they smacked of the anthropomorphism and sentimentality which they found so unscientific and so opposed to the new belief in objectivity in human and animal psychology.[45] It may also be true that their hostility to any subjectivity of this kind was a defence against the logical implications of Darwinism.[46] A rare example of the meeting of these two approaches is found in *Animal behaviour*,[47] in which Lloyd Morgan refers sympathetically to the 'victims' of 'utter hunger' of Thorndike's [too] 'strained and straitened' puzzle-box experiments;[48] although Lloyd Morgan himself had much earlier carried out cruel observations of the behaviour of scorpions when trapped in 'rings of fire'.[49] But because of his Canon (rather than any of his own animal work), Lloyd Morgan has been blamed for some of the excesses of the new, objective psychology (which he himself tried later to moderate by qualifying the Canon's use):

> As we look back now at the typical Enlightenment view that was so confidently expressed by Lloyd Morgan, ... what we see is surely a vigorous, deliberate widening of the gap between humans and all other animals. It was an antiseptic attempt to protect the human race from pollution by cutting its links with the rest of nature ... [Psychologists'] notions about the species barrier slipped right back from Darwin's emphasis on continuity towards something very close to Descartes's position.[50]

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physiologist of St Bartholomew's Hospital) who in giving evidence before the Royal Royal Commission said he only gave anaesthetics to keep the animals quiet: 'I declare to you, I did not believe the man lived, who was such an unmitigated, cynical brute as to profess and act upon such principles; and I would willingly agree to any law that would send him to the treadmill' (cited by Leffingwell, A., 1905a, The vivisection problem - a reply. *International Journal of Ethics*, XV, p.227).

[44]See his letter to the *Times* of 25 April 1881, as a 'lover of animals' but one who supported the research of Burdon Sanderson in whose laboratory he had worked. He made the common comparison between the cruelty of the field (in this case, use of the spring trap) and the lesser and excusable suffering of the laboratory.

[45]Just as the 'objective' psychologists were turning from Darwinian to learning theories, so also they reacted in their 'hard' scientific approach to the very different, but popular and competing, theories of the psychoanalysts.

[46]Ryder, R.D. (1989) op. cit., p.164.

[47]Lloyd Morgan, C. (1900) *Animal behaviour*. London: Arnold, pp.147 & 151.

[48]Warden claimed that the American Burroughs and others criticized Thorndike on sentimental grounds, and that conditions in the laboratory were supposed to approximate to those in the natural environment, which was probably harsher. Warden, C.J. (1927) The Historical Development of Comparative Psychology, *Psychological Review*, XXXIV: 135-68.

[49]Lloyd Morgan, C. (1883) Suicide of scorpions. *Nature*, 27: 313-4.

[50]Midgley, M. (1994) Bridge-building at last. In: Manning, A. and Serpell, J. (eds) (1994) *Animals*

The Universities Federation for Animal Welfare was established in 1926 as the University of London Animal Welfare Society, a scientific animal welfare society aiming 'to show that study of the welfare of animals should be a branch of scientific sociology'. It had an undergraduate and postgraduate membership, and Julian Huxley and David Katz became early vice presidents. Its aims and functions were to 'influence those who will later be leaders of society by exploiting contact they can have at university with biologists and vets; to educate public opinion; to promote accurate thinking; ...the contemptuous attitude towards animals which underlies most cruelty needs to be replaced by that broader-minded view of their nature which is deducible from biological science'. Huxley helped to promote a questionnaire addressed to field clubs and natural history societies seeking information on otters and badgers as examples of wild animals especially subject to persecution; and the Society, like the public antivivisection societies, expressed an early concern over the cruelties of trapping. Through pre-war editions of *The Animal Year-Book* the Society set out its stance on animal experiments: 'The Society is precluded by its constitution from engaging on either side in controversies relating to scientific experiments on animals.' Such a stance would facilitate without embarrassment a wider membership, and perhaps also reflected a wish to avoid fierce controversies such as that of the experimental and symbolic Brown Dog of the early years of the century, a creature which through a commemorative statue in Battersea polarized the university's medical students and opponents of vivisection. By 1938 the Society had become a Corresponding Society of the British Association for the Advancement of Science and affiliated to the Institute for the Study of Animal Behaviour. Then, after the war, as UFAW, it began to turn its attention to the position of laboratory animals, when as an organization consisting largely of scientists and academics it was seen as competent to comment authoritatively on carefully examined issues of experimental suffering, issues inevitably connected with factors related to sensation and behaviour. In November, 1947 the inaugural meeting of the Cambridge University branch took place at St John's College, when Sir Frederic Bartlett took the chair and accepted the branch presidency. Following a circular, 100 applicantions had been made to join the branch within a week, and in February the following year it organized a symposium on pain at which Bartlett and E.D.Adrian spoke, with James Gray in the chair, and when, according to the 22nd Annual Report of UFAW, the house was packed. Bartlett soon became a vice president of the Federation and at the Annual General Meeting of the

and human society - changing perspectives. London and New York: Routledge, pp.189 & 192. But Midgley's views were contradicted by those of B.E.Rollin (see above).

Cambridge branch in October 1949, again under Bartlett's presidency, George Humphrey and R.E.Rewell spoke on 'Fear in animals'.[51]

What was by 1959 the Association for the Study of Animal Behaviour invited C.W.Hume of UFAW to address it on the question of anthropomorphism.[52] Scientific societies have not often encouraged animal welfare organizations to lecture them, especially when the topic was a subject of routine familiarity to them, and the speaker being from without the discipline scientifically most competent to understand it. However, the nature of the topic of anthropomorphism allowed also for some philosophical argument, and Charles Hume was an extremely articulate author (the strength of his articles often let down by their trivial titles[53]). In his address of 1959, Hume attempted to justify anthropomorphism by stating that ability for cold reasoning was peculiar to humans whereas emotions as observed through common behavioural and nervous responses to traumatic and other stimuli were shared alike by human and non-human animals (and as supported by evolutionary theory); that intuitive imputation of feelings in animals was as legitimate as reading the significance of human feelings from, for example, facial expressions, and that in their successful interaction with animals hunters, trappers and trainers used these anthropomorphic imputations in a proven, practical way; and that there was analogous, flexible appetitive behaviour across species boundaries. Furthermore, analogies between man and animals could be found in the use of language, in electroencephalograms, in the psychosomatic effects of anxiety, and in the capacity to learn and be conditioned by reward or punishment through the intelligent and sensible formation of mental associations: 'There is no evidence ... that intelligent creatures are more sensitive than stupid ones, for the two factors [intelligence and sensibility] are confounded in experiments ... A heavy burden of proof rests on anybody who would repudiate anthropomorphism.' The difficult position is that anthropomorphic attribution of similarities between animals and man have therefore at the same time provided a rationale and value for experimental, comparative studies of animal behaviour, and resulted also in concerns such as Hume's that the similar interests of the animal should be respected. This difficulty has led to an artificial language serving a denial that an ethical problem might exist, consisting of clinical jargon (especially developed in the USA by the behaviourists) that, for example, replaces 'photoreception' for seeing, or 'vocalization' for all manner of animal communication from mating calls to screams of pain. 'When the accurate and

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[51]Copies of the Annual Reports of UFAW, together with much uncatalogued material, is kept at its headquarters in South Mimms, Potters Bar. The previous London office, together with the earlier archives, were destroyed in the blitz.
[52]Hume, C.W. (1959) In Praise of Anthropomorphism. *The UFAW Courier*, 16: 1-13.
[53]e.g. Hume, C.W. (1949) *How to Befriend Laboratory Animals*. London: UFAW.

proper use of language has entrapped a zoologist into a statement that seems to him heretical, it is quite usual to hear him apologise for speaking teleologically, and he generally looks as sheepish and embarrassed about it as if his bedroom had been found full of empty whisky bottles.'[54] It is ironic that anthropomorphism has been supressed as an experimental if not an ethical embarrassment, but that it remains the basis of comparative behavioural research, and indeed of the legislation regulating animal experiments.

Those who paved the way for the introduction into Britain of ethology were of course much more ready once again to attribute qualities of experience to animals, in spite of the aftermath of Lloyd Morgan's Canon, and then ethology itself set about demonstrating the links between human society as examined by anthropologists and the behaviour of non-human social animals (although some like Zuckerman, and the laboratory-orientated animal psychologists, would dispute any such links). Julian Huxley and W.H.Thorpe were both actively concerned not only with conservation but also with animal welfare issues, and used their academic knowledge and standing to promote these. Huxley commented on the cruelty of commercialized meat production;[55] as secretary of the Zoological Society of London from 1935 he became concerned by the cramped conditions and boredom of the animals at the Zoo; and he later speculated on the application of animal research techniques to human subjects when with his brother in 1955 he witnessed American work on the stimulation of the pleasure centres of the brain in rats.[56] Later, Thorpe served on the Brambell Committee on the keeping of domestic animals, and pioneered recognition of the cruelty of close confinement and beak-clipping.[57]

W.H.Thorpe believed that ethology could help in solving the problems of animal welfare that existed in animal experiment and husbandry:

> The problem of determining what treatment is to be allowed and what forbidden can only be solved with the help of biologists working in

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[54]Pumphrey, R.J. (1952) Ethology comes of Age. *Advancement of Science*, vol.8, pp.376-7. Cited by Hume, C.W. (1959) op. cit., p.3.

[55](1907) *Natural selection*. Unpublished essay dated 'Oxford 1907'. Julian S.Huxley Archive, Woodsen Research Centre, Fondren Library, Rice University, Texas. Early Materials, Box 2: 1906-1909. Cited by Bartley, M.M. (1995) Courtship and continued progress: Julian Huxley's studies on bird behaviour. *Journal of the History of Biology*, 28: 107.

[56]'We were stirred by a mixture of fascination and horror at the state of these poor creatures acting under a compulsive spell ... Was Aldous's Brave New World moving a step nearer?' (Huxley, J.S., 1970, *Memories*, Vol.II. London: George Allen and Unwin Ltd, p.175.)

[57]Hinde, R.A. (1987) William Homan Thorpe 1 April 1902 - 7 April 1986. *Biographical Memoirs of Fellows of the Royal Society of London*, 33: 621-39.

many different fields: but primarily those investigating the natural behaviour of animals - the branch of biology now known as Ethology ... I regard the greatest scandal of all to be our national tolerance of the current conditions of intensive animal husbandry and the near impossibility of securing a conviction of 'cruelty' against many of those responsible for the 'management' of farm animals under these conditions.[58]

At the time, in 1977, 45 million birds were kept in battery cages. In a review of the publication of a symposium on animal rights,[59] he complained: 'I am ... convinced of the cruelty of "factory farming" ... Sir Julian Huxley was right in saying when he and others wrote to *The Times* concerning the new and disgracefully feeble "Codes of Practice", issued in 1968 by the then Minister of Agriculture, "It is obvious to us that behavioural distress to animals has been completely ignored. Yet it is the frustration of activities natural to the animal which may well be the worst form of cruelty"'. Thorpe regretted that the book did not discuss the report of the Brambell Committee of 1965,[60] which was largely ignored by the Ministry of Agriculture after it had itself established the Committee with a promise to carry out its recommendations.

A council member of the RSPCA, Rev. Andrew Linzey, had invited Thorpe in January 1977 to participate in the symposium, which was intended to examine the ethical aspects of man's relationship with animals, by contributing a paper on experimentation, bloodsports or intensive farming. Thorpe offered an 'Assessment of Pain' which Ruth Harrison[61] used in her paper at the symposium. This assessment concentrated firstly on anxiety and stress (with evidence such as dogs pulling on a lead to avoid the premises of a vet where they had earlier received an injection, mice refusing to approach an area of previous shock, boredom as shown by 'weaving' in zoo animals, and discomfort in pigs attempting to carry straw to make a comfortable bed); and secondly on terror, which he felt probably not to be as severe an experience as in man because of reduced anticipation and dread, but which deserved the benefit of doubt. Thorpe's 'Assessment' also resulted from his participation in 1977 in the Animals and Ethics Working Group of the British Council of Churches, a group including biologists, theologians and veterinarians which set out to prepare an agreed

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58 Camb Univ Lib MS Room. William Homan Thorpe: Papers 1927-84. Add. MS 8784 / M13.
59 Paterson, D. and Ryder, R.D. (eds) (1979) *Animals' Rights - a symposium*. Fontwell, Sussex: Centaur.
60 *The Report of the Technical Committee to enquire into the Welfare of Animals kept under Intensive Livestock Husbandry Systems (Brambell Report) 1965*. London: HMSO. In Appendix III, Thorpe dealt with 'The Assessment of Pain and Distress in Animals'.
61 Author of *Animal Machines* (1964), London: Vincent Stuart, which had led to the setting up of the Brambell Committee that year.

statement on an ethical basis for man's relationship with animals. Having recognized man's status as a moral being involving the ability to 'conceive just ends, to reach rational conclusions and to act altruistically in response to them', Thorpe's group included in the final version of its statement: '... Animals should be regarded as possessing rights to exist within their own terms and within their own peculiar conditions of existence in virtue of their status as created beings. This principle should help to determine our treatment of animals; though it should not be regarded as absolutely binding in all circumstances. In cases where rights conflict we need to adopt reasoned criteria as a basis for judgement'. This may help to explain why, for example, Thorpe did not believe that fox hunting was necessarily cruel, since the wolf was probably an earlier predator of the fox. He also criticized publications such as Desmond Morris's *Naked Ape* for emphasizing man-animal similarities and neglecting very significant differences - linguistic, intellectual, artistic, technical, literary, moral, ethical, scientific and spiritual. Observing the status of animal welfare in the late 1970s he considered the existing laws on animal experimentation as 'good as far as they go (and they should go much further)' and conscientiously enforced as far as was possible by a much-too-small inspectorate. Improvements were needed, and 'the RSPCA has already embarked on the support of ethological and ecological research ... One of the most promising, admirable outcomes of this has been the work of Dr Marian Dawkins (1977) on the behaviour of battery-reared and farmyard chickens. This kind of support for research should be developed on a much wider and long continued scale ...'[62]

In 1928 P.T.Young had published a short note concerning 'Precautions in Animal Experimentation'. He warned his American readers of the danger of legislation restricting the experimental use of animals, of the kind that existed in Britain: 'the experience of England with such laws has clearly shown the undesirability of legislation which restricts the investigator'. He advises the adherence to codes of practice to stave off pressure for such measures in America, and an 'Open Door' policy.[63] No such article appeared at this time from British workers in animal behaviour, but C.S.Myers had earlier dealt with the subject of vivisection in the paper 'Is Vivisection Justifiable?'.[64] Myers was certainly convinced of the need for the use of animals in psychological research, and on this occasion he offered his views on physiological vivisection because:

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[62]Camb Univ Lib MS Room. William Homan Thorpe: Papers 1927-84. Add. MS 8784 / M13.
[63]Young, P.T. (1928) Precautions in animal experimentation. *Psychological Bulletin*, no.25: 487-9.
[64]Myers, C.S. (1904) Is vivisection justifiable? *International Journal of Ethics*, XIV: 312-22.

> ... the subject can be treated with the necessary impartiality only by one who, while sympathetic towards dumb creatures and having adequate knowledge of modern biological science, does not engage in the practice of vivisection; who, if he desire adequate competency, should have some general acquaintance with the principles of ethics and have the training in psychology that will help him to gauge the precise extent and intensity of animal suffering.

Myers proceeded to claim that there was 'no ground for suspecting that vivisection has a baneful effect on the temperament of those that practise it'. His interpretations were at times either naive or tactically disingenuous (and he was soundly drubbed by his protagonist in later editions of the *International Journal of Ethics*, Albert Leffingwell), as when he reassured: 'Again and again dogs have been observed to wag the tail or lick the hands of the operator, even immediately before the beginning of the experiment'. Cries, struggling etc. are the signs of pain, but 'while they are all *concomitants* of pain, it must never be forgotten that they are by no means sure *evidence* of pain ... the sentimentalist at once leaps to the conclusion that it must suffer just the feelings of distress which would be his under similar conditions. Errors of this kind are so well known to students of mental phenomena that they have been termed "the psychologist's fallacy"'. The natives of the Torres Straits were allegedly half as sensitive to pain as Englishmen, and so the greater difference in mental build in animals would make their suffering very obtuse. Myers ended his altercation with Leffingwell (an American also with medical training) by stating that he had attended many vivisections and felt sufficiently qualified alike on medical, ethical and psychological grounds to maintain with sincerity and without change his views and statements.[65] In 1927 he signed a petition to the Home Secretary, along with many other Fellows of the Royal Society and others connected with the Research Defence Society, against the Dogs Protection Bill, which was promoted by the National Canine Defence League and sought to end the use of dogs in physiological experiments.[66]

Another psychologist, G.C.Grindley, of the generation after Myers, one more directly involved in animal research, and who adopted the laboratory rather than the ethological approach to his work, expressed a different and more informed view in his *The Sense of Pain in Animals*.[67] He acknowledged the danger that in attributing too

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[65]Myers, C.S. (1905b) Discussion. The vivisection problem: a personal explanation. *International Journal of Ethics*, XVI: 235.
[66]WIHM CMAC. SA/RDS J.1/34.
[67]Grindley, G.C. *The Sense of Pain in Animals*, revised by the author and reprinted in 1959, from the original article in the *Animal Year Book*, vol.2, 1933. London: Universities Federation for Animal Welfare. A copy annotated by W.H.Thorpe, where his concurrence with Grindley's viewpoints is marked by underlinings, exists in Camb Univ Lib MS Room Add MS 8784 / M13.

much to the animal mind, a tendency which is bound to be present also among scientists when a complex mind tries to understand a simpler mind, ridicule would result for the animal welfare movement, but accepted that it was possible to estimate what certain animals feel rather than think. He distinguished pain from stress and made convincing physiological and behavioural comparisons of the signs, causes and experiences of both in humans and animals, concluding that the main difference lay in the levels of understanding and avoidance learning rather than in unpleasantness of experience.

> Evidence from behaviour can of course be judged best by someone who is thoroughly familiar with the species of animal under consideration, and who knows all the emotional expressions shown by that species. The arguments which have been given also suggest that it is right that work for the welfare of animals should, at present, be mainly concerned with mammals and birds ... The arguments for the existence of pain and suffering in animals seem unanswerable.

Very little appears in the psychological literature of the 1960s on the matter of ethical considerations in behavioural experimentation with animals. When at Oxford between the end of the 1950s and 1967, N.J.Mackintosh encountered no formal statements of ethical concern for animal welfare, although his own work, involving either invertebrates or imposing very moderate levels of hunger on rats, did not require a licence. But as psychologists, he and his colleagues, like the ethologists, believed it more difficult to obtain a just estimate of an animal's natural behaviour or capacities if that animal was severely stressed. And Mackintosh remarks:

> I can certainly recollect being shocked by procedures involved in the attempt to do electrophysiological work with octopus, and by the notably more callous attitude towards laboratory animals, that seemed to prevail in North America. Since this included keeping them in cages and conditions which would not have been tolerated in England, I assume that our standards may well have been maintained by Home Office inspection or regulations.[68]

There are occasional, passing references to humaneness[69] or to legal requirements[70] at this time, but organized discussion of animal welfare topics in science as a whole

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[68]Mackintosh, N.J. (1986) Personal communication, 10 December.
[69]e.g. Chance, M.R.A. and Mackintosh, J.H. (1962) The effects of caging. In: *Laboratory Animals Centre Collected Papers, report of a symposium held at the Royal Veterinary Laboratory on 11 April 1962, The environment of laboratory animals.* Carshalton: Laboratory Animals Centre, Medical Research Council Laboratories, p.63.
[70]e.g. Pritchatt, D. (1966) Comparative psychology as an undergraduate practical course. *Bulletin of*

appeared only to take place at the instigation of the Universities Federation for Animal Welfare.[71] In their popular literature, psychologists were keen to assure the general reader of good motives, intentions and practice. For example, P.L.Broadhurst emphasised the experimenter's responsibilities (to the welfare of his animals, to himself and to his colleagues by maintaining a safe and sanitary environment, and to the legal and moral requirements of society), and confirmed that they were invariably met. He employed anthropomorphic terminology to effect this reassurance, describing the life of the laboratory rat as one of leisured tranquillity interrupted only by occasional concern about the arrival of its next meal or some moments of fairly acute discomfort. Small cages were supposedly excused if the animal was nocturnal. Another ethical aspect of animal psychology might be the applied results of such work, but in this speculative area there was little but optimism: 'whole crops may be harvested by ape labour in the future' and what was really a technology of animal behaviour offered food for thought for industrialists who might soon employ pigeon pilots and chimpanzee engine-drivers.[72]

There were odd indications in the 1960s, however, of the disagreement that would later arise between 'experimenting' and some 'non-experimenting' psychologists (who happened very often, it was to prove, to be clinical psychologists). For example, M.B.Shapiro[73] wrote in 1965: 'The infliction of injuries on animals for research purposes presents a special problem. It would seem to be impermissible to do these things for purely academic purposes. It is only where serious questions of health in

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the British Psychological Society, 19, 65: 26 (on the need to consult with the Home Office Inspector about proposed undergraduate animal work); and Blizard, D.A. and Cochrane, R. (1967) Letter to the editor. *Bulletin of the British Psychological Society*, 20, 67: 58f. (on the need to update the Cruelty to Animals Act, 1876, so that psychological research is included in its framework and professors of psychology enabled to ratify research proposals).

[71]e.g. Keele, C.A. and Smith, R. (eds) (1963) *The assessment of pain in man and animals*. Papers given at an international symposium held under the auspices of UFAW in London in 1961. London: Universities Federation for Animal Welfare. (Reviewed by G.C.Grindley in the *Quarterly Journal of Experimental Psychology*, 1964, p.192, but no psychologists appeared to have spoken at the symposium.)

[72]Broadhurst, P.L. (1963a) *The science of animal behaviour*. Pelican Books, pp.8, 20-21, 48-49 & 135.

[73]Shapiro, M.B. (1965) An approach to the social responsibilities of the clinical psychologist. *Bulletin of the British Psychological Society*, 18, 59: 34. At this time he was working at the Institute of Psychiatry, Maudsley Hospital, where his colleague P.L.Broadhurst saw animal research in a much more enthusiastic light. Shapiro had warned a student, J.A.Gray, that there was little he could contribute to clinical psychology by doing fundamental research in the rat laboratory. In 1984, Gray was awarded the Presidents' Award of the British Psychological Society and took the opportunity of attempting to demonstrate the relevance of animal work for clinical psychology and psychiatry, for example because of the similarity of the neurology of anxiety in man and rat, and because he believed in no dichotomy between cognitive and behaviourist psychology, their being 'two sides of the same coin'. Gray, J.A. (1985) A whole and its parts: behaviour, the brain, cognition and emotion. *Bulletin of the British Psychological Society*, 38: 99-112.

man himself are involved that such operations may be justified.' But W.Sluckin[74] said of British animal behaviour studies as they had developed by 1969: 'It should perhaps be noted that probably most research in the field of animal behaviour, whatever its roots and character, is carried out for its own sake rather than with reference to any human studies'. Richard Ryder, senior clinical psychologist at Warneford Hospital, Oxford, and between 1977 and 1979 chairman of the council of the R.S.P.C.A., did much to extend the debate within psychology to the public arena in the 1970s. Before the publication of his *Victims of science* in 1975 he had asked in the *Sunday Mirror*:[75] 'Can we justify cruel experiments on animals on the grounds that psychologists can learn more about behaviour?', answering 'I do not believe any of the suffering I have caused to laboratory animals - and, alas, there has been some - has helped humanity in the slightest.' Another psychologist, Alice Heim, had written in her book *Intelligence and personality: their assessment and relationship*[76] of 'the apparent callousness of much of the experimental work carried out on the lower animals', later comparing such experimentation with the practices of Nazism. She attributed such immorality to behaviouristic and mechanistic views of mind, and observed: 'The work on "animal behaviour" is always expressed in scientific, hygienic-sounding terminology, which enables the indoctrination of the normal, non-sadistic young psychology student to proceed without his anxiety being aroused. Thus, techniques of "extinction" are used for what is in fact torturing by thirst or near-starvation or electric-shocking.'[77]

The first letter in a long series of correspondence (some of it later becoming rather acrimonious) on the ethics of the use of animals in behavioural research was published in the *Bulletin of the British Psychological Society* in August 1975.[78] Over the next four years, letters from various correspondents[79] covered a variety of aspects of the ethical question, including: the practical value of the research undertaken; whether the degree of stress involved should be left up to the experimenter; the comparative status, in terms of moral responsibility to be assumed by the experimenter, of human and non-human animals; the possible erosion of moral responsibility because of the effect of the allegedly uncaring laboratory ethos; the validity of evidence for suffering; humaneness and the lack of it; the justification of research which might be non-medical, or undertaken to achieve pure knowledge rather than knowledge directly

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[74] Sluckin, W. (1969) Animal behavioural and ethological work. *Supplement to the Bulletin of the British Psychological Society*, 22: 35-6.
[75] 24 February 1974. Cited by Ruesch, H. (1979) *Slaughter of the innocent*. London: Futura, p.255.
[76] (1970) Harmondsworth: Penguin Books.
[77] Quoted by Ryder, R.D. (1983) op. cit., p.55.
[78] Sperlinger, D. (1975) Correspondence. *Bulletin of the British Psychological Society*, 28: 356-7.
[79] These included D.Sperlinger, M.B.Shapiro, R.D.Ryder, A.Jolley, L.J.Holman and D.G.Boyle.

applicable to the alleviation of suffering in humans; the necessity or prevalence of peer-group control of stressful experiments, or of their control by assessors including non-experimenters; whether all animals should have consideration, even, for example, protozoa; the nature of controversial experiments and the nature of the stocking of animals; the possible withdrawal of recognition of animal experimentation by the British Psychological Society; the comparison with other treatments of animals, such as eating or hunting them; and, if animals possessed similarities to human beings adequate enough to make behavioural research on them valid, whether for that reason there was a moral requirement not to subject them to research involving suffering.[80] Fox[81] has succinctly dealt with the latter point, which has not been convincingly countered by supporters of severe procedures:

> To subject animals to suffering for knowledge's sake (in which there is no conceivable clinical application), is ethically reprehensible. If it is a high fidelity model, then presumably the animal is suffering much as would a human being. Yet in spite of the psychologists' claims to relevance of their animal models, they avoid ethical responsibility by discounting all concerns as being ill informed and anthropomorphic and, if such concerns are not valid, then surely the investigator is guilty of being anthropomorphic by claiming that the model is relevant to man.

At the Annual General Meeting of the British Psychological Society in Exeter in 1976, the above matters were discussed in a symposium, and as a result it was decided that the Society's Scientific Affairs Board should set up a Working Party whose terms of reference would be to examine: ways of ensuring that psychological advice was incorporated in Home Office assessments of licence applications; standards of training and supervision; the definition of 'animal' and possible categorization for purposes of assessing 'ethical cost'; the scale and economy of animal use; the nature of proper conditions for accommodation; the assessment of qualitative and quantitative 'ethical cost' in experiments, to be weighed against the likely benefits of findings; and the

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[80]One of the similarities that began to suggest itself was altruism. On 9 September 1970, the *Daily Telegraph* reported that S.J.Dimond of the Department of Psychology at the University College of Wales, Cardiff had discovered that a rat would press a lever to save another from drowning, and that a monkey would refuse a food reward if the reward resulted in an electric shock for another animal. (Cited by Ruesch, H., 1979, op. cit., p.55.) The notion of altruism in animals would appear to be the kind of anthropomorphic weakness especially criticized by the behaviourists, but by this time alternative theories for animal (and human) behaviour based on the idea of 'kin selection' and 'inclusive fitness' were beginning to compromise the simple opposition of the earlier standpoints: it might be argued that immediate conscious behaviour in animals supported such long-term evolutionary theories.

[81]Fox, M.W. (1981) Experimental psychology, animal rights, welfare and ethics. *Psychopharmacology Bulletin*, vol.17, no.2: 82.

formulation of a set of guidelines for psychological teaching and demonstrations involving animals.[82]

The Working Party presented its report in 1978, and comments were invited from other scientific societies and organizations, and, when the Report appeared in the *Bulletin of the British Psychological Society*,[83] from the B.P.S. membership. Before its publication, K.J.Connolly as chairman of the Scientific Affairs Board had submitted a draft for comment to D.H.Smyth, chairman of the Research Defence Society. He asked for confidential comments and stated: 'There is considerable pressure from some members of the Society to substantially reduce the amount of behavioural research with animals whilst of course there are many other members of the Society who are committed to continuing research programmes which involve animals as subjects'.[84] Responses from other, related scientific organizations indicated their interest in joining with the British Psychological Society in the liaison to be developed with the Home Office (as described in the terms of reference). The report itself began by outlining the nature and influence on psychological research of the 1876 Cruelty to animals Act, and continued with statistics on animal research in psychology departments in the United Kingdom, as represented by universities and polytechnics undertaking undergraduate teaching, and staff and postgraduate research. The 215 Licence holders in 38 departments of psychology had diverse degrees of contact with the 14 Home Office Inspectors, and Inspectors differed in the thoroughness with which they carried out inspections and in the experimental parameters such as shock levels which they advised laboratories to be acceptable to the Home Office. Researchers appeared satisfied with the operation of the 1876 Act, but this might have reflected a concern that modifications might impose further restrictions on their work. In training, a system of personal 'apprenticeship' in research techniques appeared satisfactory, and the behavioural characteristics of animals in their natural environments were taken into account during the organization of laboratory work. In 39 out of 57 departments, animals were used in undergraduate teaching, and in a minority of cases there was some uncertainty about the legally acceptable extent to which undergraduates could become involved in procedures. Students were usually allowed to opt out of animal work on grounds of conscience if they so wished. Teaching staff felt that students should be permitted to benefit from personal use of laboratory animals, and that films

[82](1976) Working Party on Animal Experimentation, *Bulletin of the British Psychological Society*, vol.29: 377.
[83](1979) Vol. 32: 44-52.
[84]K.J.Connolly to D.H.Smyth, 15 September 1978. WIHM CMAC: SA/RDS K4/2.

or video-recordings would be a poor substitute except in areas that involved licensable procedures.

In considering the ethical implications of animal work, the Working Party found that in spite of similarities between human and non-human animals, the differences justified the research, because, for example, animals lacked awareness and anticipation of the procedures being applied or planned; but 'these issues should continue to be the subject of public debate within the psychological community'. Broadly speaking, the aim should be maximum gain (in new knowledge or alleviation of human suffering) for minimum suffering. This might be achieved by better planning of experiments; proper advance consultation with colleagues; avoidance of unimportant or replicate work; and where possible, the use of alternatives to animals. In the interests of the economical use of animals, the requirement of the Act that animals be killed after work under anaesthesia should be altered to save those that could survive with no ill-effects; and experimenters should examine more closely the feasibility of multiple-use of animals in research. The Working Party recommended that the majority of the advice in its report concerning the potential causes of animal suffering and concerning the responsibilities of experimenters should be made more clear during courses of undergraduate instruction. It also recommended that a Standing Advisory Committee on Standards for Psychological Research and Teaching Involving Animals be established by the British Psychological Society to liaise with the Home Office over implementation of the 1876 Act; to create guidelines for training graduate students; to liaise appropriately with similar committees of other societies; and to act as an ethical watchdog. Those who did not experiment on animals should also serve on the Committee.

The Working Party had invited comments from the membership on its published report, and reactions were published in the *Bulletin* over the ensuing two years.[85] These reactions were extended to pass opinion, too, on the Committee set up (after the recommendation of the Working Party) in October 1979, which soon began discussing proposed government legislation and parliamentary bills under the chairmanship of D.E.Blackman. Those who reacted critically made accusations of insincerity, complacency and partisanship which were vigorously refuted; and the critics also repeated some of the arguments that had been made by correspondents before the Working Party's report had been published. Shortly afterwards, the British

[85]Correspondents included A.Heim, C.A.Glass, K.J.Connolly (chairman, Scientific Affairs Board), J.E.Orme (member of the Working Party), D.Sperlinger, D.E.Blackman (chairman of Standing Advisory Committee), R.L.Reid (chairman of Scientific Affairs Board in 1980), R.D.Ryder and H.Beloff.

Psychological society declined an invitation to join the Research Defence Society, but at the end of the following year (September 1983) it was announced by the Scientific Affairs Board that the newly formed Psychobiology Section of the Society was to be asked 'to advise on any role it might play in the identification of members willing to take an active part in considering the interests of psychologists conducting psychological research with animals'.[86]

In a report on the work of the Standing Committee by the Chairman, D.E.Blackman, in January 1982, it had been stated that 'further steps have been taken to develop a code of good practice in psychological teaching and research involving animals, and these efforts are now being co-ordinated with the Experimental Psychology Society and the Association for the study of Animal Behaviour. It is also hoped to co-ordinate the editorial practice of the three Societies with respect to any specific ethical issues arising from animal experiments'. To supplement the advice contained in its earlier Working Party Report, the Scientific Affairs Board issued in 1985 'Guidelines for the use of animals in research',[87] prepared jointly with the Experimental Psychology Society and based on those published by the Association for the Study of Animal Behaviour in 1981.[88] These supplementary guidelines reminded researchers of the law; ethical considerations; implications for suffering of species' natural history; economy in the use of animals; endangered species; the use of reputable suppliers; suitable caging and environment; care against disturbance in field work; the undesirability of contriving aggression and predation including infanticide; care with deprivation schedules in studies of motivation; alternatives to and reduction of aversive stimulation and stressful procedures; competence and caution in surgical and pharmacological procedures; responsibilities for anaesthesia, analgesia and euthanasia; and proper use of independent advice. The Association for the Study of Animal Behaviour published a new but similar version of its guidelines in 1986.[89] Earlier, before the publication of the common guidelines, the Experimental Psychology Society had acknowledged the restrictions necessary to enforce ethical standards by announcing in Notes for Authors in its *Quarterly Journal*: 'Research reported in this Journal is expected to conform to certain ethical standards. The editor must be the judge of those standards and reserves the right to reject, after consultation with the president of the Experimental Psychology Society, any paper reporting experiments which, in his judgement, caused

[86](1983) Monthly Report: Scientific Affairs Board. *Bulletin of the British Psychological Society*, 36: 326.
[87](1985) *Bulletin of the British Psychological Society*, 38: 289-91; (1986) *Quarterly Journal of Experimental Psycholology*, 38B: 111-6.
[88](1981) *Animal Behaviour*, 29: 1-2.
[89](1986) *Animal Behaviour*, 34: 315-8.

the subjects needless or unjustifiable suffering'.[90] In an editorial to the 1986 edition of this journal, R.A.Boakes referred to the threat to behavioural research from the animal rights movement; and to the Animals (Scientific Procedures) Bill, with its proposed Animal Procedures Committee, which would make it even more necessary for researchers to be able to define and justify their proposed work. Meanwhile, the *Journal* would not attempt to disguise the contents of research published, by means of the use of jargon less easily understood by activists who combed through such publications. Instead, researchers should begin to explain and defend the value of their work more vigorously, as has Gray;[91] and those involved in human research should acquaint themselves with and support animal work more actively.[92]

What appeared to have been a quite sudden concentration on the business of ethical considerations and procedural guidelines in the mid 1970s, and perhaps stemming from the symposium held at the British Psychological Society's conference in Exeter in 1977, resulted not just in correspondence in the *Bulletin*, but also in related articles, and activities by interested parties who wanted the subject discussed more widely. G.R.Martin[93] wrote in criticism of the traditional comparative psychology of animal learning and advocated ethology and behavioural biology as the way ahead for animal research, warning against the 'ill-informed, emotive attacks' of psychologists who did not work with animals. An article appeared on 'Research on the ethics of research';[94] and in 1980 M.W.Fox, a British ex-patriate who had undertaken many experimental studies in the United Kingdom concerned with animal behaviour, had contributed to an American Psychological Association symposium entitled 'Ethical issues in research with animals'.[95] Here he referred to further articles by S.E.G.Lea on alternatives[96] and A.Heim on morality in psychological research.[97] D.E.Blackman followed with an

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[90]'Notes for authors' (1981) *Quarterly Journal of Experimental Psychology*, 33B: i. Since 1975, the editorial notes of *Pain* had announced: 'We shall refuse to publish any reports where the animal was unable to indicate or arrest the onset of suffering'. The frequent and accepted use of terms such as 'suffering' demonstrated that the transatlantic behaviourist principles had in the end failed to overcome the subjective attributions to animals which the new, 'objective' psychology had found so unscientific earlier in the century.
[91]Gray, J.A. (1985) op. cit. J.W.Driscoll and P.P.G.Bateson (1988, Animals in behavioural research. *Animal Behaviour*, 36: 1571) also believed that support could only be expected if work was shown to be valuable and if psychologists demonstrated active concern for animal welfare.
[92]Boakes, R.A. (1986) Editorial. *Quarterly Journal of Experimental Psychology*, 38B: 1-3.
[93]Martin, G.R. (1977) Animal experiments in psychology - a prognosis. *Bulletin of the British Psychological Society*, 30: 73-5.
[94]Aitkenhead, M. and Dordoy, J. (1983) Research on the ethics of research. *Bulletin of the British Psychological Society*, 36: 315-8.
[95]Fox, M.W. (1981) op. cit.
[96]Lea, S.E.G. (1979) Alternatives to the use of painful stimuli in physiological psychology and the study of animal behaviour. *ATLA Abstracts*, 7: 20-1. Cited in Fox, M.W. (1981) op. cit.
[97]Heim, A. (1978) The proper study of psychology. *Times Higher Education Supplement*, 24

explanation of legal requirements and their implications in Britain.[98] Fox, as director of the Institute for the Study of Animal Problems in Washington D.C. (a division of the Humane Society of the United States) sent the first two issues of the new *International Journal for the Study of Animal Problems* to W.H.Thorpe, as one who had 'contributed so outstandingly as an ethologist to establish the science of animal welfare', and invited him to contribute 'a comment piece or a review article dealing with the role of ethology and of ethologists in animal welfare science ... I believe that it is particularly important to demonstrate to veterinarians and animal scientists the role that ethology can play and how important it is to include applied ethology in the college teaching curriculum'.[99] In the symposium on animal rights organized by the R.S.P.C.A., D.Sperlinger (who had himself convened the British Psychological Society's special symposium at Exeter in 1977) set out the views he had expressed concerning the responsibilities of scientists when corresponding with the *Bulletin of the British Psychological Society*; and of the Society's future policies, he was 'pessimistic about radical recommendations'.[100] Shortly afterwards, Sperlinger edited a book containing a series of articles by both scientists and philosophers on animals in research,[101] including an assessment of animal experimentation in the behavioural sciences by R.Drewett and W.Kani;[102] a chapter on 'Ethology - the Science and the Tool' by D.Macdonald and M.Dawkins; and another entitled 'The fallacy of animal experimentation in psychology' by D.Bannister.[103] More recently, P.P.G.Bateson addressed the general scientific community and interested public through the pages of *New Scientist*,[104] when he tackled the problem of weighing up the degree of suffering

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November, p.9. This article was based on a paper presented at a meeting of the British Association for the Advancement of Science in Bath on 5 September. The day after this meeting, the *Times* (p.16) reported her address under the heading 'Nazi-style animal experiments attacked'.

98 Blackman, D.E. (1981) op. cit.

99 M.W.Fox to W.H.Thorpe, 28 April 1980. Camb Univ Lib MS Room: Add MS 8784/M13.

100 Sperlinger, D. (1979) op. cit.

101 Sperlinger, D. (ed.) (1981) *Animals in research: new perspectives in animal experimentation.* Chichester: Wiley.

102 They believed that in some areas animal work had diverted effort and produced few solutions to human problems; that much American work deserved criticism by psychologists themselves, and that British publications like *Nature* should not publish such work if it were impermissible in Britain; that the legal constraints on use of animals for teaching psychology have not always been understood or applied by British academics; and that because experimental animal work in psychology has understandably and often legitimately been singled out by campaigning groups, psychologists should themselves question and cut back on such work.

103 Bannister believes that animal manipulation has become a technology, often economically driven, which contributes little to real science in psychology; that psychology is about experience rather than behaviour; that 'animal psychology' is a paradoxical notion, and 'physiological psychology' a contradiction in terms; and that the precision of experiments is spurious and negated by the very imprecision of their wider implications. He also notes in passing the erosion of moral restraint caused by the enveloping laboratory ethos, as demonstrated by Milgram's notorious 'obedience' experiments in 1965.

104 Bateson, P.P.G. (1986) When to experiment on animals. *New Scientist*, 20 February, pp.30-2.

against the value of the research.[105] He wrote in the light of a recent concerted effort by the animal rights movement against psychological and behavioural experiments, and the Animals (Scientific Procedures) Bill.[106] Justification is given for behavioural research, and mention is made of the Association for the Study of Animal Behaviour's Ethical Committee (established in 1979 and of which Bateson became secretary) and editorial policy on articles. He called for greater participation in the debate by scientists in order to defend the prospects for their work, and for a collaboration with critics so that the interests of both science and experimental animals could be served by fruitful and constructive discussion and action. Meanwhile the Association for the Study of Animal Behaviour was preparing a pamphlet to answer printed propaganda attacking behavioural research.[107]

An article by J.Archer[108] later referred to the provisions of the new Animals (Scientific Procedures) Act, and some features of the previous ten years' debate and activity concerned with the ethical considerations of behavioural research. He noted, for example, the meeting at Durham in 1980 of the Association for the Study of Animal Behaviour in order to discuss ethical issues; the harrassment of a research worker at the Maudsley Hospital;[109] and to further anti-vivisectionist commentaries.[110] Archer felt that because the activists remained intent on selecting behavioural work as a target, the British Psychological Society should strengthen its guidelines and be seen to be enforcing a mandatory code via an ethical committee. This code should be more clearly related to procedures used in psychobiological research; it should be applied when vetting conference reports of research or submissions for Society journals; and it should promote quality in research as well as the avoidance of suffering. Members would in these ways become more aware of ethical considerations; and the Society would be seen both to take the matter of ethics seriously and to defend and promote psychobiological work that it had ratified as legitimate and valuable. A code for the British Psychological Society would need to

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[105] Macdonald and Dawkins (in D. Sperlinger, ed., 1981, op. cit., p.220), of the Animal Behaviour Research Group in the Department of Zoology at Oxford, had themselves mentioned the need for moral cost-benefit analysis but that 'the out-of-context quotational evaluation is an abominable device too often employed in discussions of animal experimentation'.

[106] e.g. Sharpe, R. (1985) *Psychological and behavioural research*. London: Mobilization for Laborarory Animals against the Government's Proposals.

[107] A similar printed reply to Sharpe (op.cit.) was published by the Committee of the Experimental Psychology Society: 'The use of animals for research by psychologists'.

[108] Archer, J. (1986) Ethical issues in psychobiological research on animals. *Bulletin of the British Psychological Society*, 39: 361-4.

[109] See report in the *Guardian*, 7 October 1985.

[110] e.g. Bowd, A. (1982) Psychological research with animals. In: *Reason versus vivisection* London: International Association Against Painful Experiments on Animals.

protection of it; heated correspondence in the *Times* and *British Medical Journal*; the excitement of public opinion at a time when the second Royal Commission on Vivisection was examining and taking evidence; and, following the refusal of Battersea Borough Council to remove the monument after representations from University College, its mysterious disappearance in 1910.[113] Coleridge himself carried into the twentieth century a representation of the emotive anti-scientific stance which had developed especially among some religious, well-heeled and classically educated members of society during the previous decades. He was scathing of Darwinism's threat to human dignity and Huxley's championing role as an 'uncouth pedagogue of Science', and protested at:

> ... the sterile steps of exact knowledge that deflate all they tread upon ... the prostrate attitude of the modern world before this new and terrible Deity ... Science has toiled early and late to destroy beauty and banish it from human life. It has given us machine carving and the Post-Impressionists! ... Thought, which was once the panoply of an immortal soul, it has pronounced to be no more than a particular condition of some grey matter in the cranium ... these things matter more to us than the origin of species, the excretions of earthworms, the methods of locomotion, the facilities for communicating words, or the battles of bacteria, none of which can elevate the character or purify the heart ... This sinister advance of Science, which is desolating all things lofty in life, is the great and dominant event of the last fifty years; if it continues unchecked it will lead down to a general disintegration and dissolution of Society, which, after all, is entirely based on the unscientific qualities of subordination, duty, mercy, reverence, love, and willing toil for the benefit of others.[114]

In 1948 the Duchess of Hamilton, together with the British Union for the Abolition of Vivisection, the National Anti-Vivisection Society and other anti-vivisection societies, presented a co-ordinated petition to the Home Secretary demanding a new Royal Commission to investigate animal experiments, and using in support of the petition seven examples of licensed research which was deemed unacceptable. The petition was rejected because the Home Secretary believed that the Act was working adequately, but only after the Home Office had sought explanations from the relevant scientists to put alongside the Duchess of Hamilton's seven statements. One of the seven examples used was an experiment for which G.Ungar and S.Zuckerman had received a licence on 3 April 1943, to study, in relation to the Blitz, traumatic shock, using a rotating drum and other methods, and involving rats, guinea-pigs and other animals. By 1948

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[113]Univ Lond, UC MS Lib: Item 36.
[114]Coleridge, S.W.B. (1913) *Memories*. London: John Lane.

Ungar had returned abroad again, but Zuckerman explained that the animals were under anaesthetic at the time.[115] A few years later Lord Dowding began a debate in the House of Lords resulting from his call for an inquiry into the 'entirely new conditions' which had arisen since the issue of the report of the Royal Commission of 1912 and which were characterized by what he believed to be useless experiments. Some such experiments involved the testing of the efficacy of drugs and toxins by studying their effects on the behaviour of animals in the laboratory.[116]

During recent decades attention has been extended very decisively in the direction of behavioural research, perhaps for two main reason, these being firstly the campaigners' need to maintain a difficult and long-standing struggle by identifying a 'softer' (because usually non-medical) target; and secondly because some behavioural work has been perceived not only as unnecessary, but also trivial, sinister, particularly callous or cowardly [117] and more easily open to comment from the layman who feels he knows something of the 'common sense' of psychology (but could not pretend to be able to comment knowledgably on, say, physiology). Television has since the 1960s

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[115]It was not made clear, however, whether the animals were allowed to recover from the anaesthetic instead of being destroyed, which would have been the normal requirement of the Act, but which would have presumably compromised this behavioural experiment. The 'rotating drum' referred to was probably what came to be known as the 'Noble-Collip Drum', a new device perhaps used in Britain for the first time by Zuckerman, which had been invented the year before by the two Toronto scientists of the same names. They first described it in 1942 in the *Quarterly Journal of Experimental Physiology* (vol.31, 3: 187): 'A quantitative method for the production of experimental traumatic shock without haemorrhage in unanaesthetized animals'. The animal would be traumatized by placing it in a revolving drum '... in which are projections or bumps ... The number of animals dying showed a curve in proportion to the number of revolutions.' This enduring method was later classed as unacceptable by W.D.M.Paton (1979, Animal experiment and medical research: a study in evolution. *Conquest*, 169), chairman of the Research Defence Society, alongside the American studies of 'learned helplessness' developed by Martin Seligman.

[116]The Parliamentary Debates (Hansard) Fifth Series, House of Lords Official Report, 1952, vol. CLXXVIII, no.98, columns 631-58.

[117]The animal rights movement has not hesitated to draw analogies between the situation of laboratory animals and the inhumane and tyrannical treatment of large numbers of faceless and helpless human victims in the concentration camps, or between the treatment of the vulnerable animal and the vulnerability of the child or the mentally impaired. The 'might is right' assumption has also come under increasing scrutiny as the public is asked to consider, in the light of policies concerning laboratory animals, its expectations in the event (not now so outlandish) of links with a more powerful and equally exploitative alien civilization. By 1985, leading pressure groups had combined to produce for the public, politicians and media an emotionally-charged pamphlet arguing a ban on psychological and behavioural experiments (R.Sharpe, 1985, op. cit.). In reply, the Committee of the Experimental Psychology Society issued a report on 'The use of animals for research by psychologists' in which it was said: 'It would be extraordinary if society were to encourage scientists to investigate the nature of matter and the structure of the gene, but then forbid research into the activity of mind and of the brain on which it depends.' The report set out to deal with the charges of triviality, repetitiveness, irrelevance to humans and failure to use human clinical studies instead of animal experiment, by cataloguing current research interests; and it sought to correct misconceptions about 'brain damage', electric shock and food deprivation.

engaged and promoted the public's interest in animal behaviour, primarily in natural contexts, through a growing number of natural history documentaries.[118] These have often served to encourage the notion of human kinship with animals and, like the continuing experience of caring for 'pets', effected an 'ethical bridge-building',[119] if not a new tendency to anthropomorphism, and to draw attention to the vulnerability of the animals in terms of the behaviour of humans towards them threatening extinction, destruction of habitat, commercial exploitation, etc.[120] Since the late 1970s issues concerning animal welfare have also become more politicized as pressure groups have made use of the sensitivity of politicians' awareness of electoral advantage in this area.[121] The Darwinian concept of mental continuity between man and animals has therefore been effectively expressed and articulated in new ways partly attributable to the ability of mass communication in the late twentieth century to influence the conscience of British society and to enable the individual to develop an informed world-view in which the interdependence and responsibilities affecting human and non-human animals has been made clear. The public response to its own understanding of environmental, behavioural and even moral relationships linking it to the interests of the life of animals is stronger and more influential than the other Darwinian concept of natural selection affecting the evolution of physical form, and it was this concept that originally attracted the most attention and controversy in the nineteenth century. The implications of Darwin's theories supporting mental continuity and the gradual evolution of self-consciousness, language, problem-solving and analytical ability were not fully taken up in Britain in the late nineteenth and early twentieth centuries, and most aspects of them were ignored in the United States. More recently, the public has acquired an implicit, rather than explicit, understanding of them, the irony of which is that the experimental opportunities they originally suggested (and which were not properly developed) are now, because of them, seen as morally questionable by the informed layman. It is this recently developed and widespread interest in the

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[118] J.W.Driscoll and P.P.G.Bateson (1988, op. cit., p.1570) thought that opponents of animal work should remember that such programmes were the result of ethological research.

[119] Serpell, J. and Paul, E. (1994) Pets and the development of positive attitudes to animals. In: Manning, A. and Serpell, J. (eds) (1994) *Animals and human society - changing perspectives.* London and New York: Routledge, p.129.

[120] This awareness was soon matched and articulated by the arrival of international pressure groups such as Friends of the Earth and Greenpeace, which harnessed the environmental idealism that began especially to permeate the educated and youthful elements of western society from the 1960s. A.N.Rowan and B.E.Rollin (1983, Animal research - for and against: a philosophical, social, and historical perspective. *Perspectives in Biology and Medicine*, vol.27, no.1: 9) refer to the legacy of the social criticism of the 1960s, affecting also philosophers and scientists, and to the growth of concern about various kinds of discrimination.

[121] From within Parliament, Lord Houghton fostered the campaign to 'put animals into politics' which led in 1978 to the General Election Co-ordinating Committee for Animal Protection, soliciting new policy statements from the parties.

man-animal behavioural relationship that has ensured that psychological and behavioural investigations occupy the critical attention of the onlooker. The ethical implications of physical and mental continuity had earlier been addressed by Thomas Hardy in a letter of 1910:

> Few people seem to perceive fully as yet that the most far-reaching consequence of the establishment of the common origin of all species is ethical; that it logically involved a readjustment of altruistic morals by enlarging as *a necessity of rightness* the application of what has been called 'The Golden Rule' beyond the area of mere mankind to that of the whole animal kingdom. Possibly Darwin himself did not perceive it, though he alluded to it. While man was deemed to be a creation apart from all other creations, a secondary or tertiary morality was considered good enough towards the 'inferior' races; but no person who reasons nowadays can escape the trying condition that this is not maintainable.[122]

For many intellectual antivivisectionists both sides of the turn of the century, vivisection meant the failure of the spiritual evolution of humanity.[123] As society became more secular in the following decades, and as society became less inclined to respond to pronouncements on moral rights and wrongs issued by major public figures, the autonomy of science and its ability to regulate its own procedures as it saw fit have been secured, and fewer prominent commentators now feel it appropriate publicly to oppose vivisection and behavioural experimentation on moral grounds: this opposition has rather been taken up by some 'ordinary' people or by those with a directly relevant specialism, especially since the mid-1970s and as public opinion has become better informed and accepted as a legitimate source for moralizing. Critical public views have been reinforced by some within science who have echoed lay concern about some aspects of recent and contemporary experimentation. Michael Balls, chairman of the trustees of the Fund for the Replacement of Animals in Medical Experiments, has identified five types of experiment which should not be tolerated anywhere in any circumstances whatsoever. Of these, two are psychological and the third frequently psychological: isolation in monkeys and 'learned helplessness' in dogs; aversive stimuli (e.g. electric shocks) in 'behavioural training' in psychological and behavioural research; and any experiments on chimpanzees, 'our closest relatives, which possess many qualities once thought to be uniquely human'.[124]

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[122]Thomas Hardy, letter dated 10 April 1910, in Hardy, F.E. (1962) *The Life of Thomas Hardy*. London: Macmillan, p.349.

[123]But some opponents, such as Cardinal Manning and Lord Shaftesbury, would not have thought in terms of the spiritual evolution of humanity because of their religious conservatism.

[124]Balls, M. (1988) The weighing of benefit and suffering. *FRAME News*, 20: 1-2. Nottingham:

There is therefore little evidence that behavioural research in Britain was constrained by the effect of public opinion, organized or otherwise, until recently, particularly from the 1970s, when widespread attention was brought to bear on psychology and the other disciplines it had begun to serve (notably pharmacology). This decade saw the articulation of new pressure groups frustrated with the failure of the longer-established organizations to achieve their ends and the appearance of some influential publications which helped to keep the spotlight on behavioural work.[125] Evidence of the growth in pressure especially on behavioural research is found in the sudden appearance also at this time of lengthy correspondence and special meetings related to ethical matters within the psychological community itself, as discussed above; and some experimenting scientists from other disciplines began to feel that their supposedly more legitimate activities were being adversely affected by the heat generated by lay hostility to behavioural work with animals. The work of Arnold Chamove at Stirling University, funded by the Science Research Council in the late 1970s, on maternal deprivation in monkeys, was publicly dismissed in the media by a psychiatrist, James Tulips, who claimed: 'If all such experimentation ended today, psychological and human knowledge would not be significantly impoverished'.[126] Similarly, readers of the *New Scientist* were angered not just by Nicholas Humphrey's impairment of the sight of a monkey by surgical removal of the visual cortex, but by his indifference to the animal after the operation, when it was neglected as a result of other calls on his time and left in a small cage for ten months.[127] Colin Blakemore's neurophysiological work on the development of visual perception in cats at Oxford and Cambridge has made him not only a lasting special target for militant animal rights campaigners, but also the recipient of criticism from scientific colleagues.[128]

The thoughts and publications of philosophers such as Midgley (1973), Clark (1977) and Singer (1975) helped both to legitimize and maintain the focus on issues surrounding the man-animal relationship, and to provide a disciplined framework within which logical argument and better communication could begin to replace emotive altercation. This was an important practical service of philosophy, since, as

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[125] e.g. Ryder, R.D. (1975) op. cit.; Ruesch, H. (1979) op. cit.

[126] Hollands, C. (1989) op. cit., pp.129f.

[127] Later he admitted: 'Some years ago I made a discovery which brought home to me dramatically the fact that, even for an experimental psychologist, a cage is a bad place in which to keep a monkey. Since that time, in working with laboratory monkeys I have been mindful of the possible damage that may have been done to them by their impoverished living conditions' (quoted by Hollands, 1989, op. cit., p.136).

[128] e.g. L. Goldman (1977) in the *Doctor*. Cited by Hollands, C. (1989) op. cit.

Rollin observed in 1985,[129] more had been written in the past ten years on the moral status of animals than in the previous 3,000. T.L.S.Sprigge[130] knew that philosophy could supply the animal rights movement with the rationality necessary to support a moral view. Because of the historic links between psychology and philosophy, philosophers such as Midgley[131] did not hesitate to address issues relevant to both subjects, as when she implied that 'rat psychology' offered far less than good ethology in comparative work, for which it was necessary to recognize both the entire character of the species concerned and the known principles governing resemblances between species; and the nature of a species consisted in 'a certain range of powers and tendencies, a repertoire, inherited and forming a fairly firm characteristic pattern, though conditions after birth will vary the details quite a lot'. Sprigge[132] went further in rejecting laboratory methods by suggesting that 'behaviourism and physicalism are essentially elaborations of that view of the world which underlies immorality, and that they are expressions on the philosophical scene of a general climate of opinion about the nature of men and animals which I suspect helps sustain at least some experimentalists on animals in their insensitivity and cruelty'. Such views are reminiscent of those attributed by some modern historians to the anti-vivisection movements of the late nineteenth century, which are alleged to have consisted of people fighting against a scientocratic and materialistic view of the world.[133] Since the 1960s there has occurred another form of disenchantment with science based on an awareness of its questionable social, economic and environmental effects and its traditional but unfashionable insistence on remaining as 'value-free' as possible. According to Rollin, the remoteness and power of science have alienated working people, who have come to identify militantly with those others they see as oppressed by the society it has helped to produce, namely laboratory animals.[134] Although moral philosophers from the 1970s onwards appeared usually to be aligned with the cause of animal rights, by the 1980s (and, again, perhaps appropriately for the culture of the decade in question) counter-arguments had arisen within their own quarter, as from R.G.Frey.[135]

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[129]Rollin, B.E. (1985) The moral status of research animals in psychology. *American Psychologist*, vol.40, no.8: 922.

[130]Sprigge, T.L.S. (1979) Metaphysics, physicalism, and animal rights. *Inquiry*, 22: 102.

[131]Midgley, M. (1973) The concept of beastliness: philosophy, ethics and animal behaviour. *Philosophy*, 48: 112 & 128.

[132]Sprigge, T.L.S. (1979) op. cit., p.139.

[133]e.g. French, R.D. (1975) *Antivivisection and medical science in Victorian society*. Princeton: University Press; Rupke, N.A. (ed.) (1990) *Vivisection in historical perspective*. London: Routledge.

[134]Rollin, B.E. (1989) *The unheeded cry: animal consciousness, animal pain and science*. Oxford: University Press, pp.108, 169 & 170.

[135](1982) *Interests and rights: the case against animals*. Oxford: Clarendon Press.

CONCLUSION

The present study has argued that the progress of modern experimental studies of animal behaviour in Great Britain can be associated with four historic phases. The first of these occupied the last quarter of the nineteenth century, and witnessed pioneering theoretical development supported by some innovative experimentation, both of which received inadequate encouragement from the British establishment. The British academic achievement was then routed through Lloyd Morgan and Thorndike into American science. The differing relationships linking science, government and society in United States enabled the initiative in animal psychology to be transferred effectively from Great Britain.

The considerable modification of the subject in the United States and the emphasis there on learning theory and conditioning, leading to Behaviourism, marked a divergence from areas of interest preferred in Great Britain, where a second phase of comparative quiescence in active animal behaviour studies then occupied the period from the early 1900s to the 1940s. However, in this period of academic retrenchment, institutional arrangements for the later reinvigoration of animal behaviour studies were set in place, and at the same time the first stirrings occurred of work contributing to the forthcoming leading British role in European ethology. The second historical phase is therefore suitably seen as a preparatory one.

Between the 1940s and 1960 the fruits of pre-war American work were imported into Great Britain, when a period of absorption and application took place, involving also a realignment of the difficult relationship between animal psychology and ethology, and the consolidation of professional developments in the form of new societies and journals. Animal behaviour studies assumed new importance in areas of applied science, sometimes now in a commercial or industrial environment, and helped to serve research and development in those professions and disciplines with medical or economic value.

The 1960s and 1970s, the fourth historical phase proposed in this study, were marked by considerable intitutional expansion, and academic development and diversification at an international level, often resulting in further doubts over the identity of comparative (as opposed to general animal) psychology as it became eclipsed by the evolving neurosciences and as laboratory based animal studies became increasingly associated with the service of other, primary interests in cognate disciplines. A proliferation of research work became subject to the conditioning of public scrutiny and ethical criticism, during which, ironically in a period of highly sophisticated, objective and complex scientific analysis, philosophical commentary and the old questions about the moral basis of the man-animal relationship began to reappear. British work early in this final period had led to developments in genetic theories which contributed to the growth of interest in sociobiology as a new international subject emanating from the USA. Meanwhile the secure foundations of ethology had been recognized as a worldwide discipline by the simultaneous award of the Nobel Prize in 1973 to three workers including Tinbergen of Oxford. In this period a rapprochement and sharing of methods between comparative psychology and ethology left the latter with greater academic independence and the former with a role increasingly approximated to the technical support of other disciplines.

This work has examined the the nature of the British response in the late nineteenth century to the possibilities opened up to comparative psychology by an experimental application of developed aspects of Darwinian theory. The significance for the emerging science of the studies carried out is established, and at the same time the influence of the external social, religious, political and institutional environment on the prosecution by key figures of their investigations is analysed. The importance of the immediate academic environment is also assessed, and appropriate comparisons made, for example, with associated and sometimes competing academic subject areas, and with the contrasting research ethic existing in Germany.

The circumstances under which at the beginning of the new century Great Britain lost the lead to the USA in studies of animal behaviour therefore become clear, and the legacy of reliance in such innovative (but economically less urgent) research areas on amateur or gentleman-scientist enthusiasm is contrasted with the enthusiastic application of the fruits of the British groundwork by salaried American academics. They very soon neglected the Darwinian rationale and concentrated on a new form of research in animal psychology, sanctioned by the domestic establishment which provided a stimulating market for work in learning theory serving the needs of national education policy and social control and improvement. Such willingness to attempt to use applied science either to improve or manipulate society was soon echoed in the USSR, as when Pavlov was recruited to help regulate society through his work on conditioning, but it represented a role for science that was alien to Britain.

British studies of animal behaviour had become objective, easily communicable and replicable well before the time of Hobhouse's last experiments, and these were readily exported into a new social, cultural and scientific milieu where experimental techniques were then intensively developed to create a new scientific movement, Behaviourism, which American science could promote and call its own, and which came to emphasize a continuing inertia in the field in Great Britain. The transfer of activity to the USA also marked a change in the way that experimental work was undertaken. Animal psychology became less comparative, and a concentration on stimulus-response, learning theories and conditioning drew attention away from Darwinian preoccupations. The experimental study of instinct became unfashionable, and the discursive approach of the earlier British anecdotalists was frowned upon as the American workers set about the task of creating a hard, objective science free of those nineteenth century embellishments so characteristic also of much general Victorian culture. It has been shown that, ironically, British influence played an unwitting part in this change of emphasis and experimental style, through the exaggerated adoption of Lloyd Morgan's Canon in the USA. Meanwhile, the new, positivist American approach proved unattractive to a cautious and conservative British academic establishment, in which psychology was still regarded as bound by philosophical interpretations of the human mind rather than by the strategies of a biological science. Indeed, the academic status in Britain of laboratory work in animal psychology may well have become tarnished by its all too easy association with that of the American behaviourists.

The early history of the international study of animal behaviour reveals a series of oscillations in the manner in which investigations were conceived and carried out, and British work may now be placed retrospectively into this context. After the publication of Darwin's *The expression of the emotions in man and animals* in 1872, the time suggested as the beginning of the modern school of animal behaviour studies,[1] an anecdotal phase predominated in Britain before more procedurally exact scientific enquiries shifted via Lloyd Morgan and Hobhouse to the United States of America, leaving a lull in Britain. Studies of animal behaviour in the closing decades of the nineteenth century were carried on by a limited number of gentlemen and non-establishment scientists, among whom there were good communications as well as a willingness to involve a general public readership in their work. Sometimes this tendency to poularization, which could be seen as an aspect of the Victorian duty on the part of the knowledgeable to serve 'improvement,' had negative results, as when in

[1]Thorpe, W.H. (1956) Some implications of the study of animal behaviour. *The Advancement of Science*, XIII, 50: 42-55.

a manner that has remained a characteristic of the scientific world, the worth of Romanes's important work came to be judged mainly on the basis of his popular writings.[2] The surrounding political, religious and educational contexts were not encouraging for a new science, especially one with strong tendencies to materialism and reflecting sensitivities over the dignity of man, factors which would inevitably provoke a reaction in Victorian society, however hypocritical in terms of actual religious belief that society might be. It has been noted that at the outset of his career in the 1900s, Frederic Bartlett was fully aware of this unsympathetic environment, but decided to face it in necessarily unconventional, 'cranky' [his term] and non-conformist style.

The relatively quiescent period of 1900 to 1940 has traditionally been dismissed as of little significance in Great Britain, but the first university departments, staff establishments and laboratories for animal behaviour were then formed. It is less remarkable that Britain should have lost the lead than that the USA should have provided the conditions in which the subject could flourish. Great Britain did have a special place as the home of Darwin, but no other country than the USA vigorously developed scientific animal behaviour studies in the early decades of the new century. The continental development of ethology was a parallel but different and shared area of development, with the British work of Julian Huxley and Edward Russell meanwhile helping to prepare the subject for its later status as a generally European one. They re-adopted the Darwinian and instinctive standpoints, rejecting American learning theory and Behaviourism and advocating a zoological approach.

By the 1930s, Russell was stressing the value of observation and recording as opposed to exploitative collecting or the use of unnatural control in the artificial conditions of the laboratory. His was a philosophical approach to practical studies in animal behaviour which in many ways presaged the environmental ethics of the 1960s and 1970s, by which time in Britain ethology had become a European subject, symbolically under Tinbergen encouraging closer relations between psychology and zoology. In the

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[2]The engagement of public interest has since proved most influential on the progress of animal behaviour studies, not without problems for the individuals involved. Academic disapproval was expressed over Julian Huxley's use of the press to attract interest in his work on the axolotl, but his eagerness, like that of his father, to inform the public of the value of science was shown by his collaboration with (the anti-behaviourist) H.G.Wells in the publication of *The Science of Life* in 1930. More recently, and with the advent of mass communications, it has become expected of scientists that they communicate, explain and even justify the value of their work to public audiences. The criticism now sometimes levelled is that of commercial popularization which might affect academic honesty and accuracy. Desmond Morris has received such criticism: he is much better known for his popular and somewhat speculative publications than for his important academic work, but in the 1950s and 1960s he successfully maintained an appreciative public focus on his subject.

mid-1970s some scientists began to lend support to new social and philosophical concerns over the morality of some forms of animal behaviour study, concerns often based ironically on those Darwinian theories which had been neglected in the United Kingdom because of the socio-political environment of science at the turn of the century, and in the USA because they were less relevant to the growing interest there in new learning theories. Such concerns are shown to have been absent in earlier decades,[3] but the interest in them in the 1970s contributed to a spate of overt self-regulation on the part of the specialist societies and a redrafting of controlling legislation which became a feature of the 1980s.[4]

At the turn of the century the opportunities for a physiological psychology as a biological science, through collaboration with accomplished and sympathetic neurophysiologists such as Sherrington and then Adrian, were ignored, partly because of the conservatism or philosophical orientation of psychologists themselves. But just as the initiative in controlled experimentation swung from Britain, so too was there a swing from prospects of study based on Darwinian theory to the associationist / connectionist psychology of Thorndike's America, and to Pavlovian reflexology, finally leading to Behaviourism, trends tending to serve an establishment market for the intended methodical education, improvement and control of American society. The neglect of physiological psychology in Britain meant that the ground was never prepared for the acceptance of radical schools of thought of this type, although through the work of E.M.Smith and G.C.Grindley at Cambridge knowledge of them existed in circles where strategic research decisions were made. British work therefore remained until the 1940s sporadic and (in comparison with that in the United States of America) 'soft', and the avenues opened up by the late nineteenth century pioneers were abandoned. Furthermore, these pioneers had not operated within a university context, and so their work had become, and remained for some time, associated by the scientific community with a range of uncoordinated and 'amateur' lines of enquiry in a subject that needed (and received in the USA) an exemplary line of approach with some establishment support.

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[3]For example, N.J.Mackintosh recalls that in the late 1950s suffering in laboratory animals was avoided because it might spoil the results of experiments, 'but this belief was not translated into any formal procedure for soliciting ethical concern or monitoring the treatments and procedures we adopted.' Mackintosh, N.J. (1986) Personal communication, 10 December.
[4]On 2 November 1978 the *Times* had reported, under the heading 'Reappraisal of animal experiments urged' (p.6), that Bernard Dixon, editor of *New Scientist*, supported the critical comments of Alice Heim at a symposium of the R.S.P.C.A. on animal experimentation. He called for a public enquiry and an examination of animal experimentation by the Commons Select Committee on Science and Technology, noting the 'poor level of discussion of the subject in the House of Commons' at the time.

Behaviourism was methodologically strong but theoretically weak, and failed to elucidate complex behaviour, although with it the USA, in contrast to Great Britain, achieved a school of animal behaviour studies that became the focus of attention and energy for several decades, an achievement that met the requirements of a 'reputational system' and provided the framework for thoroughgoing institutionalization and professionalization. In opposition to behaviourism, a continental reaction in the form of Gestalt psychology produced another oscillation in ideas. For their part, Lloyd Morgan and Hobhouse had taken the middle ground between the (public) anecdotalism of Romanes and the opposite extreme of a mechanistic-physiological view of animal behaviour. They had recognized the value of good field study but understood also the necessity of experimental investigation as a means of solving some specific problems. Then they turned to other interests, and animal psychology in Britain would have been forlorn between 1900 and 1920 but for the continued attention given to it by the women psychologists at Cambridge and London. These women (E.M.Smith, Beatrice Edgell and Victoria Hazlitt) opened the second phase in the history of the development of the subject in the United Kingdom, following the close of the first with Hobhouse. Their circumstances and motives have been described as indicative of the socio-political climate of their times: they can be considered in the much wider context obtaining then of uncertainty about the place and meaning of science in society and about the funding of it. In this context and until the 1940s, experimental studies of animal behaviour were limited and received little official, institutional or public recognition.

The strange but original attempts, ahead of their times, to train animals to locate submarines during the First World War involved not animal psychologists, but circus trainers working under the direct supervision of a marine biologist with specialist knowledge of the structure and physiology of the ear of whales, dolphins, sea-lions, and seals.[5] The Admiralty's use soon after of Cambridge staff for hydrophone personnel selection and training, who were themselves responsible for overseeing animal work in the Cambridge Psychological Laboratory, demonstrates that a sufficient network existed for the employment of animal psychologists, had that been preferred. But the application of psychological expertise did not extend into this area,

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[5]It was noted in Chapter 3 of this work that Victoria Hazlitt had made reference to circus training when writing on learning in man and animals. It is suggested that a new and fruitful area for future research might consist of an examination of the methodological links between traditional practice in the circus and the laboratory based procedures that were developed by and after Edward Thorndike. In this way, the aspect of animal psychology based on learning theory and experiment could be compared with historical, non-scientific developments in intensive animal training that was undertaken for entirely different purposes.

and in another, concerned with the identification, acceptance and treatment of what later came to be known as shell shock, the psychologists' analysis was resisted.

After the conclusion of hostilities, the improved recognition of the role of science in society, in the economy and in the universities was soon thwarted by the effects of the depression. Meanwhile, those who had pioneered modern studies of animal behaviour in the late nineteenth century were not now available or willing to promote their subject, and the priorities of psychologists in strategic positions within the universities lay elsewhere. Prospects for particular avenues of research within psychology were dependent on the interests of individuals such as Charles Myers and Frederic Bartlett whose principal enthusiasms did not include studies of animal behaviour. Politically, concentration remained centred on the more established and economically productive sciences and technologies, and research opportunities remained restricted, especially in comparison with the USA and Germany. Through the 1920s and into the 1930s there was no equivalent in Great Britain of that faith in the ability of science to help shape and improve society which resulted in the USA in the establishment support of the development of applied learning and behavioural theories. Furthermore, the adventurous social and scientific outlooks in the USA continued to be affected by a unique and growing variety of scientific and cultural traditions reflected in its cosmopolitan population. Meanwhile, and with the exceptions of Juian Huxley and Edward Russell, work in British prototype ethology still depended on many of those who reflected the amateur or gentleman-scientist tradition.

The Second World War inevitably reaffirmed the value of applied science, and this included greater recognition of the practical use of studies of animal behaviour, which began to diversify across academic boundaries. These uses developed rapidly to serve, for example, medicine, pharmacology and agriculture, whereupon behavioural studies often assumed the form of secondary techniques designed to provide data for a primary area of research and development. Some of the research now took place on commercial premises, and its laboratory orientation, which owed much to the procedural refinements developed in the USA in the previous 40 years, helped to make ethological field studies of animal behaviour for its own sake more distinct. The demand for progress in the laboratory typified by Research Council programmes was matched by growing lay interest in field work, stimulated by accessible and expanding television coverage from the late 1950s.[6] Work both in the laboratory and in the field

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[6]A full analysis of the strategies and funding of the Research Councils from their inception, and linked to the output of work in the present subject area, would represent a worthwhile development of this research topic by further elucidating the place of animal behaviour studies in national science

was also beginning to be professionalized and internationalized by improvements in communications and collaboration soon after the war's end, most clearly shown by the appearance or consolidation of new specialist societies and journals. As much laboratory-based animal psychology became subservient to other areas of investigation, and ethological theory and method gained influence, the relevance of comparative psychology was now brought into question, and its independent status later became precarious with the development of the neurosciences, psychogenetics and sociobiology.[7]

During the post-war altercations between ethology and comparative psychology, Thorpe felt it was time to return to Lloyd Morgan's careful combination of both an objective and a subjective approach.[8] This would suppress the sort of oscillation that had so far made the paths of enquiry so divergent. However, over thirty years later this characteristic pattern of enquiry had not changed and the oscillations had remained evident, reflecting emphases on genetic and environmental themes in the process of evolution. 'The emergence of socioecology led to a renewed interest in social complexity and social relations as biotic systems responsive to ecological factors. The development of sociobiology once more emphasized the importance of genetic determination and stressed the analysis of behavioural adaptation as strategic,' and latterly, sociobiological theories have been seen to require 'a more extensive development of socioecological and ecocultural field study' and 'a more holistic model of adaptation which relates environmental, societal and cultural processes to those of genetic selection.'[9] Looking back once more to Lloyd Morgan, Thorpe[10] believed that 'apart from his famous Canon' his 'real claim to immortality is his development of the idea of emergent evolution and the contribution his thinking made to the concept of holism' in the world of living things: many of his statements remained entirely valid.

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policies. In the same way, a more detailed assessment could be made of the historic links between the subject in its various evolving forms and the public, by investigating the nature and effect of the different media used to promote understanding of animal behaviour studies and related issues.

[7]See, for example, Lockard, R.B. (1971) Reflections on the fall of comparative psychology. *American Psychologist*, 26: 168-79; and Wilcock, J. (1972) Comparative psychology lives on under an assumed name - psychogenetics! *American Psychologist*, June, pp.531-8. An example of the attempt at this time to reassert the relevance of comparative psychology internationally is Tobach, E., Adler, H.E. and Adler, L.L. (eds) (1973) Comparative psychology at issue. *Annals of the New York Academy of Sciences*, vol. 223, 28 December.

[8](1956) op. cit.

[9]Crook, J.H. (1989) Introduction: Socioecological paradigms, evolution and history: perspectives for the 1990s. In: Standen, V. and Foley, R.A. (eds) (1989) *Comparative socioecology: the behavioural ecology of humans and other mammals*. Oxford: Blackwell, p.30.

[10](1956) op. cit.

APPENDIX I

Individual papers on animal behaviour published or abstracted in:
Bulletin of Animal Behaviour (1938-51 inclusive)
British Journal of Psychology (1940-59 incl.)
Behaviour and Behaviour Supplements (1948-59 incl.)
Quarterly Journal of Experimental Psychology (1949-59 incl.)
British Journal of Animal Behaviour (1953-7 incl.)
Animal Behaviour (1958-9 incl.), with details of -
a. Author b. Work base c. Field of interest
d. Animals used e. Journal in which paper recorded
f. Date of publication g. Reference number.

Notes:
i) Essays, and papers on field observation or purely physiological work, are not included.
ii) Keys to the four coded categories (b-e) are supplied below (pp. 318-344).
iii) The linking of partners in authorship can be made via the reference number.
iv). Some authors were foreign visitors, but all work recorded here was carried out in the U.K. or its waters.
v). Changes of name through marriage have not been identified or indicated.

a	b	c	d	e	f	g
Allen, M.D.	A9	7	3	B26	1955	1
Allen, M.D.	A9	7	3	B26	1956	2
Allen, M.D.	A9	7	3	B26	1957	3
Allen, M.D.	A9	7	3	A12	1958	4
Allen, M.D.	A9	7	3	A12	1959	5
Allen, M.D.	A9	7	3	A12	1959	6
Allen, M.D.	A9	7	3	A12	1959	7
Amoroso, E.C.	L55	33	7	B26	1957	8
Andjus, R.K.	L31	32	7	Q1	1956	9
Andrew, R.J.	C12	25	6	B26	1956	10
Andrew, R.J.	C12	11	6	B26	1956	11
Andrew, R.J.	C12	7	6	B9	1956-7	12
Andrew, R.J.	C12	22	6	B9	1956-7	13
Anthony, W.S.	O7	15	7	Q1	1958	14
Ball, J.N.	L9	5	5	B26	1954	15
Banks, C.J.	H2	8	3	B26	1954	16
Banks, C.J.	H2	38	3	B26	1955	17
Banks, C.J.	H2	8	3	B26	1957	18
Barnett, S.A.	L29	7	7	B9	1951	19
Barnett, S.A.	G4	8	7	B26	1953	20
Barnett, S.A.	L29	8	7	B26	1953	21

Barnett, S.A.	G4	8	7	B9	1956	22
Barnett, S.A.	G4	11	7	A12	1958	23
Barnett, S.A.	G4	25	7	B29	1958	24
Barrass, R.	N14	5	3	B9	1959-60	25
Barrass, R.	N14	12	3	B9	1959-60	26
Barraud, E.M.	C12	3	5	B26	1955	27
Barraud, E.M.	C2	5	2	B26	1957	28
Bastock, M.	O14	5	3	B9	1955	29
Bastock, M.	O15	12	3	B9	1958	30
Bastock, M.	L39	5	3	A12	1959	31
Bell, F.R.	L55	8	7	B26	1957	32
Bell, F.R.	L55	33	7	B26	1957	33
Bell, F.R.	L55	33	7	B26	1957	8
Berlyne, D.E.	S1	25	7	B29	1950	34
Blest, A.D.	C12	11	6	B26	1955	35
Blest, A.D.	C12	11	3	B9	1957	36
Blest, A.D.	C12	11	3	B9	1957	37
Blest, A.D.	L64	11	3	A12	1958	38
Blest, A.D.	L64	11	3	B9	1958	39
Blest, A.D.	O15	12	3	B9	1958	30
Braude, R.	R6	7	7	B33	1946	40
Broadhurst, P.L.	L51	25	7	B29	1957	41
Broadhurst, P.L.	L51	25	7	B29	1958	42
Broadhurst, P.L.	L51	25	7	B29	1958	43
Brownlee, A.	C27	7	7	B33	1950	44
Butler, C.G.	H2	3	3	B9	1952	45
Butler, C.G.	H2	3	3	B9	1955	46
Carthy, J.D.	L53	21	3	B9	1951	47
Carthy, J.D.	L53	21	3	B9	1951	48
Chance, M.R.A.	G7	35	7	B33	1946	49
Chance, M.R.A.	B18	35	7	B9	1948	50
Chance, M.R.A.	B21	35	7	B33	1948	51
Chance, M.R.A.	B21	25	7	B9	1950	52
Chance, M.R.A.	B21	22	7	B26	1953	53
Chance, M.R.A.	B21	35	7	B26	1953	54
Chance, M.R.A.	B21	25	7	B26	1954	55
Chance, M.R.A.	B21	11	7	B9	1955	56
Chance, M.R.A.	L72	7	8	B26	1956	57
Chance, M.R.A.	B18	4	7	A12	1958	58
Chapman, R.F.	L42	24	3	B26	1954	59
Chitty, D.	O16	7	7	A12	1958	60
Clark, R.B.	B37	2	2	A12	1959	61
Clarke, J.R.	O16	2	7	B9	1956	62
Clarkson, J.K.	O7	15	7	Q1	1959	63
Clarkson, J.K.	O7	19	7	Q1	1959	64
Cole, J.	O9	19	8	B9	1954	65
Cole, J.	O9	38	8	B9	1957	66
Crook, J.H.	C12	5	6	B26	1957	67
Crowcroft, P.	O16	7	7	B9	1955	68
Crowcroft, P.	T1	3	7	B26	1955	69
Cutts, J.	L42	15	7	B29	1957	70
Danziger, K.	O7	27	7	Q1	1951	71
Danziger, K.	O7	27	7	Q1	1953	72
Davis,D.E.	N11	7	7	B9	1955	73

Delany, M.J.	E11	7	3	A12	1959	74
De Ruiter,L.	015	11	3	B9	1952	75
Deutsch, J.A.	07	5	7	B26	1957	76
Deutsch, J.A.	07	15	7	Q1	1958	14
Deutsch, J.A.	07	19	7	Q1	1958	77
Deutsch, J.A.	07	15	7	Q1	1959	63
Deutsch, J.A.	07	19	7	Q1	1959	78
Deutsch, J.A.	07	19	7	Q1	1959	64
Dobson, R.M.	H2	8	3	A12	1959	79
Dodwell, P.C.	L42	19	7	B26	1956	80
Dodwell, P.C.	L43	19	7	B29	1957	81
Donald, H.P.	E2	10	7	B26	1954	82
Downing, B.M.	S12	8	6	A12	1959	83
Duckworth, J.E.	N4	38	7	B26	1955	84
Duckworth, J.E.	N4	8	7	A12	1958	85
Duckworth, J.E.	N4	8	7	A12	1958	86
Dunnett, G.E.	C12	28	6	B26	1953	87
Eayrs, J.T.	B19	36	7	B26	1953	88
Eayrs, J.T.	B19	38	1	B26	1954	89
Eayrs, J.T.	B19	22	7	B26	1954	90
Eayrs, J.T.	B19	36	7	B26	1955	91
Eayrs, J.T.	B19	32	7	A12	1959	92
Edwards, J.T	P2	7	7	B33	1946	93
Edwards, R.L.	017	5	3	B9	1955	94
Edwards, R.L.	Hio	5	3	B26	1955	95
Ellis, P.E.	L64	7	3	B9	1953	96
Ellis, P.E.	017	7	3	A12	1959	97
Empson,D,W,	W3	5	3	B9	1950	98
Finlayson, L.H.	B25	5	3	B9	1950	99
Fraser, A.F.	P9	2	7	B26	1957	100
Free, J.B.	H2	3	3	B9	1952	45
Free, J.B.	H2	3	3	B9	1955	101
Free, J.B.	H2	3	3	B9	1955	46
Free, J.B.	H2	5	3	B26	1955	102
Free, J.B.	H2	21	3	B26	1955	103
Free, J.B.	H2	8	3	B26	1956	104
Free, J.B.	H2	8	3	B26	1957	105
Free, J.B.	H2	8	3	B26	1957	106
Free, J.B.	H2	21	3	A12	1958	107
Free, J.B.	H2	3	3	B9	1958	108
French, R.A.	H2	32	3	B26	1957	109
Gabbutt, P.D.	E10	5	3	B26	1954	110
Gill, J.C.	B39	6	7	B26	1956	111
Glow, P.H.	L67	35	7	Q1	1957	112
Glow, P.H.	L67	35	7	A12	1959	113
Glow, P.H.	L67	35	7	B29	1959	114
Godfrey, J.	E8	3	7	A12	1958	115
Goldacre, R.J.	L39	22	2	A12	1958	117
Goodman, L.	L52	24	3	A12	1959	118
Goodwin, D.	P9	1	6	B9	1952	119
Gordon, J.G.	B39	8	7	B26	1954	120
Graham, T.C.	A9	8	7	B26	1954	120
Graham, W.M.	L49	9	3	A12	1958	121
Grant, E.C.	B18	4	7	A12	1958	58

Green, R.T.	L57	38	7	A12	1958	122
Gruneberg, H.	L57	10	7	B26	1954	123
Guiton, P.	E3	13	6	A12	1959	124
Guiton, P.	O14	5	5	B9	1959-60	125
Gunter, R.	L22	24	7	B29	1950	126
Haldane, J.B.S.	L60	11	4	B9	1954	127
Haldane, J.B.S.	L60	25	5	B26	1956	128
Hall, M.F.	O14	7	6	B9	1955	129
Halley, R.J.	N8	8	7	B26	1953	130
Haskell, P.T.	L49	5	3	B26	1953	131
Haskell, P.T.	L49	38	3	B26	1954	132
Haskell, P.T.	L49	1	3	B26	1957	133
Haskell, P.T.	L49	5	3	A12	1958	134
Healey, E.G.	A11	11	5	B33	1948	135
Hinde, R.A.	O13	7	6	B9	1952	136
Hinde, R.A.	C12	5	6	B9	1953	137
Hinde, R.A.	C12	28	6	B26	1953	87
Hinde, R.A.	C12	5	6	B9	1955	138
Hinde, R.A.	C12	5	6	B26	1955	139
Hinde, R.A.	C12	13	6	B26	1955	140
Hinde, R.A.	C12	6	6	B9	1956	141
Hinde, R.A.	C12	7	6	B9	1956	142
Hinde, R.A.	C12	1	6	A12	1958	143
Hinde, R.A.	C12	5	6	A12	1959	144
Hinde, R.A.	C12	36	6	A12	1959	145
Holm, E.O.	L21	5	6	B26	1953	146
Hoogland, R.	O14	11	5	B9	1956-7	147
Humphrey, G.	O7	25	7	B33	1948	148
Hunter, I.M.L.	O7	19	7	Q1	1952	149
Hunter, I.M.L.	O6	24	7	B26	1953	150
Hurwitz, H.M.B.	L23	15	7	B26	1953	151
Hurwitz, H.M.B.	L43	38	7	Q1	1953	152
Hurwitz, H.M.B.	L43	15	7	Q1	1954	153
Hurwitz, H.M.B.	L43	15	7	Q1	1955	154
Hurwitz, H.M.B.	L43	24	7	B26	1956	155
Hurwitz, H.M.B.	L43	27	7	B26	1956	156
Hurwitz, H.M.B.	L42	15	7	B29	1957	70
Hurwitz, H.M.B.	L43	15	7	Q1	1957	157
Hurwitz, H.M.B.	L43	38	7	A12	1958	158
Hurwitz, H.M.B.	L43	17	7	Q1	1958	159
Jones, J.W.	L9	5	5	B26	1954	15
Kalmus, H.	L57	8	3	B26	1954	160
Kalmus, H.	L57	8	3	B26	1954	161
Kalmus, H.	L65	25	7	B26	1955	162
Kerkut, G.A.	C3	22	2	B9	1954	163
Kerkut, G.A.	S17	22	2	B9	1955	164
Kerkut, G.A.	S17	32	2	B9	1958	165
Kerruish, B.M.	S23	5	7	B26	1955	166
Khairy, M.	L63	32	7	Q1	1956	167
Khairy, M.	L63	32	7	Q1	1957	168
Khairy, M.	L67	35	7	Q1	1959	169
Khalifa, A.	C13	5	3	B9	1950	170
Kirkman, F.B.	S7	5	6	B33	1944	171
Klopfer, P.H.	C12	19	6	A12	1959	172

Klopfer, P.H.	C12	19	6	B9	1959	173
Knight-Jones, E.W.	B5	7	2	B26	1953	174
Knopfelmacher, F.	L51	17	7	Q1	1952	175
Knopfelmacher, F.	L63	15	7	Q1	1953	176
Knopfelmacher, F.	L31	32	7	Q1	1956	9
Knopfelmacher, F.	L63	32	7	Q1	1956	167
Lane-Petter, W.	L25	38	1	B26	1953	177
Lawlor, M.M.	L40	10	7	B26	1956	178
Lawn, A.M.	L55	8	7	B26	1957	32
Lawn, A.M.	L55	33	7	B26	1957	8
Lawn, A.M.	L55	33	7	B26	1957	33
Lishman, W.A.	B19	36	7	B26	1955	91
MacGregor, E.G.	C13	21	3	B9	1948	179
Manning, A.	O14	5	3	B9	1955	29
Manning, A.	O14	8	3	B9	1956	180
Manning, A.	O14	21	3	B9	1956	181
Manning, A.	E8	5	3	A12	1959	182
Manning, A.	E8	5	3	A12	1959	31
Manning, A.	E8	5	3	B9	1959-60	183
Marler, P.	C12	4	6	B26	1955	184
Marler, P.	C12	4	6	B26	1955	185
Marler, P.	C12	7	6	B9	1956	186
Marler, P.	C12	2	6	B26	1956	187
Marler, P.	C12	2	6	B9	1957	188
Marler, P.	C12	2	6	B26	1957	189
Matthews, G.U.T.	C1	21	6	B9	1952	190
Maynard Smith, J.	L64	5	3	B26	1956	191
Mead, A.P.	B21	11	7	B9	1955	56
Mellanby, E.	M10	25	7	B33	1948	192
Mellanby, K.	H2	32	3	B26	1957	109
Moore, N.W.	B37	3	3	B9	1952	193
Moore, N.W.	B37	5	3	B9	1952	194
Moore, N.	W1	3	3	B26	1955	195
Morris, D.	O14	5	5	B9	1952	196
Morris, D.	O14	5	5	B9	1955	197
Morris, D.	O14	5	6	B9	1955	198
Morris, D.	O14	5	6	B9	1955	199
Morris, D.	O14	11	5	B26	1955	200
Morris, D.	O14	1	6	B9	1956	201
Morris, D.	O14	11	5	B9	1956-7	147
Morris, D.	O14	5	6	B9	1957	202
Morris, D.	O14	1	6	B9	1957	203
Morris, D.	O14	5	5	B9	1958	204
Moulton, D.G.	B19	38	7	A12	1958	205
Moynihan, M.	O10	5	6	B9	1953	206
Moynihan, M.	O14	5	6	B9	1955	207
Moynihan, M.	O14	7	6	B9	1955	129
Osborne, R.	E3	5	6	B26	1956	208
Phillips, R	A10	8	7	B33	1946	209
Pretty, R.G.F.	L51	15	7	Q1	1951	210
Ragge, D.R.	L12	1	3	B26	1955	211
Ranwell, D.S.	S12	8	6	A12	1959	83
Reid, R.L.	E5	15	6	Q1	1952	212
Reid, R.L.	A6	17	1	B29	1958	213

Renier,G.J.	P9	1	7	B26	1956	214
Ribbands, C.R.	H2	1	3	B26	1953	215
Ribbands, C.R.	H2	21	3	B26	1953	216
Rowell, J.	L43	27	7	B26	1956	156
Russell, R.W.	L51	15	7	Q1	1951	210
Russell, R.W.	L63	32	7	B26	1956	217
Russell, R.W.	L31	32	7	Q1	1956	9
Russell, R.W.	L63	32	7	Q1	1956	167
Russell, R.W.	L63	32	7	Q1	1957	168
Russell, W.M.S.	O14	5	4	B9	1955	218
Russell, W.M.S.	O14	5	4	B9	1959-60	219
Rzoska, J.	O16	8	7	B26	1953	220
Salzen, E.A.	D6	13	6	A12	1959	221
Shirlaw, D.W.	N4	8	7	B26	1955	84
Shirlaw, D.W.	N4	8	7	A12	1958	85
Shirlaw, D.W	N4	8	7	A12	1958	86
Simmons, K.E.L.	P9	2	6	B9	1955	222
Sluckin, W.	D6	13	6	A12	1959	221
Smith, A.V.	L31	32	7	Q1	1956	9
Smith, K.G.V.	W3	5	3	B26	1955	98
Speirs, N.	H2	21	3	B26	1953	216
Spencer, M.M.	L29	7	7	B9	1951	19
Spencer, M.M.	L29	8	7	B26	1953	21
Spurway, H.	L26	11	7	B9	1953	223
Spurway, H.	L60	11	4	B9	1954	127
Spurway, H.	L60	25	5	B26	1956	128
Steven, D.M.	E8	13	6	B26	1955	224
Stewart, J.	L43	17	7	Q1	1958	159
Stokes, B.	H2	10	3	B26	1955	225
Sudd, J.H.	D2	1	3	B26	1957	226
Sutherland, N.S.	O7	19	2	A12	1959	227
Tayler, J.C.	S21	8	7	B26	1953	228
Taylor,D.J.R.	S17	32	2	B9	1958	165
Thompson, H.V.	O16	8	7	B33	1948	229
Thompson, H.V.	O16	38	7	B26	1953	230
Thomson, W.	B39	6	7	B26	1956	111
Thorpe,W.H.	C1	21	3	B9	1950	231
Thorpe, W.H.	C12	6	6	B9	1956	141
Tinbergen, N.	O14	11	5	B9	1956-7	147
Tinbergen, N.	O14	7	6	B9	1959-60	232
Tribe, D.E.	B36	8	7	B26	1954	233
Tribe, D.E.	B39	8	7	B26	1954	120
Trotter, J.R.	O7	15	7	Q1	1956	234
Trotter, J.R.	O7	38	7	Q1	1956	235
Trotter, J.R.	O7	15	7	Q1	1957	236
Tugendhat, B.	O14	8	5	B9	1959-60	237
Vince, M.A.	C12	6	6	B9	1956	141
Vince, M.A.	C12	8	6	B26	1956	238
Vince, M.A.	C12	15	6	A12	1958	239
Vince, M.A.	C12	13	6	B29	1959	240
Vince, M.A.	C8	13	6	B9	1959-60	241
Vowles, D.M.	C3	33	3	B26	1954	242
Vowles, D.M.	R3	21	3	A12	1958	243
Walker, D.M.	R6	6	7	B33	1950	244

Wallace, G.K.	R3	24	3	A12	1958	245
Wardrop, J.C.	C29	8	7	B26	1953	246
Warren, R.P.	C12	5	6	A12	1959	144
Warren, R.P.	C12	36	6	A12	1959	145
Wasserwogel, E	L43	38	7	A12	1958	158
Weidmann, R.	O10	6	6	A12	1958	247
Weidmann, U.	O14	5	6	B26	1956	248
Weidmann, U.	O10	13	6	B26	1956	249
Wiedmann, U.	O10	6	6	A12	1958	247
Wells, G.P.	L57	28	2	B26	1953	250
Wells, M.J.	N11	19	2	A12	1959	251
Wheeler, M.R.	O15	11	4	B26	1956	252
Wheeler, R.	O6	11	4	A12	1958	253
Wood-Gush, D.G.M.	E3	5	6	B26	1954	254
Wood-Gush, D.G.M.	E3	2	6	B26	1956	255
Wood-Gush, D.G.M.	E3	5	6	B26	1956	208
Wood-Gush, D.G.M.	E3	2	6	B26	1958	256
Wood-Gush, D.G.M.	E3	5	6	A12	1958	257
Wood-Gush, D.G.M.	E3	10	6	A12	1959	258
Yaxley, D.C.	B21	35	7	B33	1948	51
Yaxley, D.C.	B21	25	7	B9	1950	52
Yudkin, J.	L63	32	7	Q1	1956	167
Yudkin, J.	L63	32	7	Q1	1957	168

APPENDIX II

Output of Centres of Animal Research, 1960 - 1971

a. Centre of research or collaborating centre (collaborating centres providing only technical support are marked *).

b-f. Numbers of experimental papers published by authors from each centre (occasionally in collaboration with authors from other centres), appearing in: b. Animal Behaviour, c. Behaviour, d. Quarterly Journal of Experimental Psychology, e. British Journal of Psychology, with f. showing the total.

g. Number of different authors per centre.

a	b	c	d	e	f	g
Anti-Locust Research Centre, London	6	3	0	0	9	5
Archbishop Holgate's Grammar School, York	2	0	0	0	2	2
Bethlem Royal Hospital, Primate Behaviour Research Centre, Institute of Psychiatry, Beckenham, Kent	4	1	0	0	5	3
British Museum (Natural History)	0	1	0	0	1	1
*British Transport Commission Research Department	1	0	0	0	1	1
Chelsea College of Science and Technology, Departments of Botany and Zoology	3	0	0	0	3	2
Fisheries Laboratory, Lowestoft	1	0	0	0	1	1
Freshwater Biology Association, Ambleside	1	0	0	0	1	1
Hill Farming Research Organization, Edinburgh	1	0	0	0	1	2
Imperial Chemical Industries	1	0	0	0	1	1
Institute of Neurology, Psychological Laboratory, Queen's Square, London	0	2	4	0	6	4
King's College (Universities of Durham and Newcastle-upon-Tyne): Dove Marine Laboratory, Cullercoats	0	4	0	0	4	2
Marine Biological Association U.K., Plymouth	1	0	0	0	1	1
Marine Science Laboratories, Menai Bridge, Anglesey	0	1	0	0	1	1
Marine Station, Millport, Isle of Cumbrae	3	0	0	0	3	2

Infestation Control Laboratory, Ministry of Agriculture, Fisheries and Food, Worplesdon	1	1	0	0	2	3
Ministry of Agriculture, Fisheries and Food, London	2	0	0	0	2	4
Nature Conservancy, Furzebrook Research Station	1	0	0	0	1	1
Pest Infestation Laboratory, Agricultural Research Council, Slough	4	0	0	0	4	2
Poultry Research Centre, Agricultural Research Council, Edinburgh	16	6	0	0	22	11
Queen's University Belfast: Department of Psychology	2	0	3	1	6	2
Rothamsted Experimental Station, Harpenden, Herts	7	6	0	0	13	12
Rowett Research Institute, Aberdeen	1	0	0	0	1	1
Royal College of Advanced Technology, Salford	1	0	0	0	1	2
Royal Veterinary College, London: Department of Physiology	1	0	0	0	1	1
St Luke's College, Exeter	0	1	0	0	1	1
Sunderland Polytechnic	0	1	0	0	1	1
Tropical Stored Products Centre, Slough	1	0	0	0	1	1
Uffculme Clinic, Birmingham: Ethology Laboratory	0	2	0	0	2	2
University of Aberdeen, Marischal College, Bee Research Department, College of Agriculture	2	0	0	0	2	1
University of Aberdeen, Department of Psychology	2	0	0	0	2	4
University of Birmingham, Department of Anatomy	7	2	2	0	11	7
*University of Birmingham, Department of Electrical Engineering	1	0	0	0	1	1
University of Birmingham, Sub-Department of Ethology, Department of Psychiatry, Medical School	2	0	0	0	2	2
University of Birmingham, Departments of Pharmacy and Medical Biochemistry	0	2	0	0	2	2
University of Birmingham, Department of Psychology	1	0	0	0	1	1
University of Bristol, Department of Psychology	3	1	0	2	6	4
University of Bristol, Department of Zoology	7	4	0	0	11	5
University of Cambridge, Department of Anatomy	1	0	0	0	1	2
*University of Cambridge, Department of Engineering	1	0	0	0	1	1
University of Cambridge, Department of Zoology	11	0	0	0	11	10

University of Cambridge, Sub-Department of Entomology, Entomological Field Station and Agricultural Research Council Unit for Insect Physiology, Department of Zoology	4	2	0	0	6	4
University of Cambridge, Sub-Department of Animal Behaviour, Department of Zoology, Madingley	34	13	1	0	48	30
University of Cambridge, Department of Psychology	15	1	15	1	32	18
*University of Cambridge, Statistical Laboratory	3	0	0	1	4	4
University College, Cardiff, Department of Psychology	3	0	0	0	3	3
University College, Cardiff, Department of Zoology	1	0	0	0	1	1
University College, Swansea, Department of Zoology	2	0	0	0	2	3
University of Durham, Department of Psychology	12	2	2	0	16	12
University of Edinburgh, Department of Physiology, Medical School	1	0	0	0	1	2
University of Edinburgh, Department of Psychology	1	0	0	0	1	2
University of Edinburgh, Department of Zoology	14	4	0	0	18	9
University of Exeter, Department of Psychology	0	0	6	1	7	7
University of Exeter, Department of Zoology	0	1	0	0	1	1
University of Glasgow, Department of Veterinary Medicine	2	0	0	0	2	3
University of Glasgow, Department of Zoology	2	1	1	0	4	4
University of Hull, Department of Psychology	11	0	3	3	17	9
University of Hull, Department of Zoology	1	1	0	0	2	2
University of Keele	1	0	0	0	1	1
University of Leeds, Department of Psychology	2	0	0	2	4	2
University of Leicester, Department of Psychology	4	0	1	2	7	10
University of Liverpool, Department of Genetics	0	1	0	0	1	1
University of Liverpool, Department of Zoology	4	4	0	0	8	4
University of Liverpool, Marine Biological Station, Port Erin, Isle of Man	2	0	0	0	2	1
University of Liverpool, School of Veterinary Science	2	0	0	0	2	1

University of London, Bedford College, Department of Psychology	0	2	0	0	2	2
University of London, Birkbeck College, Department of Psychology and Animal Behaviour Laboratory	4	0	3	4	11	8
University of London, Imperial College, Departments of Zoology and Applied Entomology, and Sirex Biological Control Unit, Field Station, Silwood Park, Ascot	2	1	0	0	3	3
University of London, University College, Galton Laboratory	2	0	0	0	2	1
University of London, Institute of Psychiatry, Maudsley Hospital, Denmark Hill	7	1	1	3	12	12
University of London, King's College, Department of Zoology	1	0	0	0	1	1
University of London, Queen Mary College, Department of Zoology and Comparative Physiology	5	0	0	0	5	5
University of London, University College, Department of Anatomy	4	2	2	0	8	4
University of London, University College, Department of Pharmacy	0	0	1	0	1	1
University of London, University College, Department of Psychology, Medical Research Council Unit for the Experimental Investigation of Behaviour	3	3	1	0	7	5
University of London, University College, Departments of Zoology and Comparative Anatomy	1	4	0	0	5	3
University of Manchester, Department of Psychology	0	0	0	1	1	1
University of Nottingham, Department of Psychology	0	0	1	0	1	1
University of Nottingham, Department of Zoology	0	1	0	0	1	1
University of Newcastle-upon-Tyne, Department of Psychological Medicine	1	0	0	0	1	1
University of Newcastle-upon-Tyne, Medical Research Council Demyelinating Diseases Research Unit, Royal Victoria Infirmary	1	0	0	0	1	1
University of Newcastle-upon-Tyne, Department of Zoology	3	0	0	0	3	4
University of Oxford, Department of Zoology	13	9	0	0	22	13
University of Oxford, Departments of Zoology and Comparative Anatomy	0	7	0	0	7	3
University of Oxford, Edward Grey Institute of Field Ornithology, Department of Zoology	0	4	0	0	4	1

University of Oxford, Hope Department of Entomology, University Museum	2	0	0	0	2	2
University of Oxford, Institute of Experimental Psychology	12	0	10	6	28	15
University of Reading, Department of Psychology	2	0	0	1	3	4
University of St Andrews, Department of Natural History, Queen's College, Dundee	2	0	0	0	2	3
University of Sheffield, Department of Genetics	1	0	0	0	1	1
University of Sheffield, Department of Psychology	7	1	1	1	10	8
University of Sussex, School of Biological Sciences and Laboratory of Experimental Psychology	4	2	11	0	17	14
University of York, Department of Biology	0	2	0	0	2	3
Water Pollution Research Laboratories, Stevenage	2	0	0	0	2	2
Zoological Society of London, Regent's Park	0	3	0	0	3	3

APPENDIX III

Authors publishing individually or jointly at least six papers between 1960 and 1971 in one or more of: *Animal Behaviour*; *Behaviour*; *Quarterly Journal of Experimental Psychology*; *British Journal of Psychology*. Details below are given in the following order: name; number of papers; dates and centres at which papers prepared; subjects of papers; animals used.

Andrew, R.J.:6

1961: Edward Grey Institute of Field Ornithology, Dept. of Zoology, Univ. Oxford	Communication	Blackbird
1966: School of Biological Sciences, Univ. Sussex	Precocious adult behaviour	Chick

Bird, M.W.:6

1963-4: Dept. of Psychology, Univ. Durham	Visual stimulation	Chick

Connolly, K.J.:7

1964; 1966-71: Dept. of Psychology, Univ. Sheffield	Imprinting	Chick
	Sexual and reproductive behaviour	
	Genetics of behaviour	*Drosophila melanogaster*
	Locomotion	
	Social behaviour	

Cowey, A:6

1961-7: Psychology Laboratory, Univ. Cambridge	Brain lesions	
	Perimetry	Monkey
	Motivation	
	Habituation	

Ellis, P.E.:6

1961-3: Anti-Locust Research Centre, London	Social behaviour	Locust

Ewing, A.W.:7

1961-9: Dept. of Zoology, Univ. Edinburgh	Sexual and reproductive behaviour Genetics of behaviour	<u>Drosophila melanogaster</u>

Free, J.B.:7

1961-70: Rothamsted Experimental Station, Harpenden	Aggression Foraging and ingestion Communication	Honey-bee
	Aggression Sexual and reproductive behaviour	Bumblebee

Hinde, R.A.:14

1961-71: Sub-Department of Animal Behaviour, Dept. of Zoology, Univ. Cambridge, and M.R.C. Unit for the Development and Integration of Behaviour, Madingley	Locomotion Response to stress Parental-filial behaviour Ontogeny	Monkey
	Sexual and reproductive behaviour	Canary
	Parental-filial behaviour	Chick
	Aggression	Fish

Hurwitz, H.M.B.:6

1961-5: Dept. of Psychology, Birkbeck College, Univ. London	Reinforcement (positive) Habituation and extinction Avoidance learning Discrimination learning	Rat

Lill, A.:6

1964-8: A.R.C. Poultry Research Centre, Edinburgh	Sexual and reproductive behaviour Aggression Social spacing	Domestic fowl

Mackintosh, N.J.:9

1963-9: Institute of Experimental Psychology, Univ. Oxford	Discrimination learning Habituation and extinction	Rat
	Discrimination learning	Octopus
	Habituation and extinction	Goldfish

McFarland, D.J.:7

1965; 1968-9: Institute of Experimental Psychology, Univ. Oxford 1966: Dept. of Psychology, Univ. Durham	Social behaviour Foraging and ingestion Discrimination learning Motivation Evolution and survival value	Barbary dove

Sheldon, M.H.:7

1967: Psychology Laboratory, Univ. Cambridge 1968-9: Dept. of Psychology, Univ. Hull 1970: Depts of Psychology, Univs Reading and Hull	External stimulation Reinforcement (positive) Discrimination learning Ontogeny	Rat

Sluckin, W.:7

1961: Dept. of Psychology, Univ. Durham 1967-71: Dept. of Psychology, Univ. Leicester	Ontogeny Imprinting Evolution and survival value	Chick

Smith, F.V.:11

1960-6: Dept. of Psychology, Univ. Durham	Visual stimulation Parental-filial behaviour	Chick Sheep

Spencer-Booth, Y.:7

1964-71: Sub-Dept. of Animal Behaviour, Dept. of Zoology, Univ. Cambridge, and M.R.C. Unit for the Development and Integration of Behaviour, Madingley	Parental-filial behaviour Ontogeny Social behaviour Locomotion	Monkey

Sutherland, N.S.:15

1960-6: Institute of Experimental Psychology, Univ. Oxford	Visual stimulation Discrimination learning	Rat
1966-9: Laboratory of Experimental Psychology, Univ. Sussex	Visual stimulation Visual stimulation Habituation and extinction	Octopus Goldfish

APPENDIX IV

Individual papers on animal behaviour recorded in Behavioural Biology Abstracts, Volume 1, 1973, with details of: a. Author's name b. Work base c. Field of interest d. Animals used e. Journal in which paper published, and f. Abstract reference number.

Notes:
i) Keys to the four coded categories (b-e) are supplied below (pp. 318-344).
ii) Names of sole authors are asterisked. The linking of partners in authorship can be made via the abstract reference number.
iii) Some authors were foreign visitors, but all work recorded here was carried out in the U.K. or its waters.
iv) Changes of name through marriage have not been identified or indicated.
v) Columns g. to m. show consecutively the number of abstracts made of each author's work in the following years' editions of Animal Behaviour Abstracts, Volumes 2 (1974) to 7 (1979) inclusive.
vi) Column n. shows the total number of abstracts made of each author's work between the sample years 1973 and 1980 (inclusive), also taking into account information from Appendix VI.

a	b	c	d	e	f	g	h	j	k	l	m	n
Adam, J.H.	C17	13	6	A12	1791							1
Adams, C.E.	C4	2	7	L1	1096							3
Adams, C.E.	C4	2	7	J34	2044							
Aitken, P.P.*	O4	23	7	P19	386		2					3
Allen, K.L.	D6	23	6	E9	370							1
Allen, S.E.	B1	23	6	J7	1476							1
Andrew, R.J.*	S28	36	6	A12	1759	2	4	2	3		2	16
Archer, J.*	S29	36	6	B6	1762	2	3	3	6	1	1	21
Archer, J.*	S29	36	6	B6	2723							
Archer, J.*	S29	38	7	A12	3285							
Archer, M.E.*	Y1	7	3	I2	3114				1			3
Atkinson, R.J.A.	I1	28	2	H1	1537	1	2		1			6
Baldwin, B.A.	C1	38	7	P7	1382	2	2	5	5	2	2	26
Baldwin, B.A.	C1	23	7	A12	1485							
Baldwin, B.A.	C1	16	7	P7	2890							
Barber, G.J.	B24	35	7	D3	1698							1
Bardner, R.	H2	9	3	E2	2225							1
Barnes, H.	O1	21	2	J17	396							1
Bateson, P.P.G.	C12	19	6	B9	978	5	7	1	4		3	26
Bateson, P.P.G.	C6	30	6	B21	2618							
Bell, E.T.	M12	5	7	A12	2105							1

Bellamy, D.	C20	1	7	J14	1063	1						2
Bermant, G.	B9	5	6	A12	1151		1					2
Bernays, E.A.	L14	40	3	E2	1398		1			4	1	8
Berryman, J.C.	L5	19	6	A12	977	3		1	2	1		9
Biederman-Thorson, M.	P9	31	6	J13	1565							1
Bitterman, M.E.	A3	16	5	B3	839	1	3	6	2		3	16
Blackman, D.E.	B24	16	7	J36	1884	2	1	7	6		1	18
Blakemore, C.	C10	31	7	N2	1576	2	1	1	2	2	1	10
Blaxter, J.H.S.*	O1	23	5	J16	367	1					1	4
Blundell, J.E.	L30	31	7	A12	475	1				1	2	9
Blundell, J.E.	L4	35	7	N7	2675							
Boakes, R.A.*	S27	15	6	J36	2794	2	3		1	2		12
Booth, D.A.*	S27	35	7	J11	114	4	9	3		4	4	33
Booth, D.A.*	S29	35	7	P7	118							
Booth, D.A.*	S27	23	7	P7	382							
Booth, D.A.*	S27	30	7	P7	609							
Booth, D.A.*	S27	35	7	P7	674							
Booth, D.A.*	S27	35	7	P7	1718							
Booth, D.A.*	B24	16	7	J11	1866							
Boyden, C.R.*	L47	9	2	M4	280							1
Brady, J.*	L49	23	3	B34	339	2	3					7
Brain, P.F.*	S31	31	7	B6	53	1	1	1	2	2	10	30
Brain, P.F.*	S31	7	7	P19	1209							
Brain, P.F.*	S31	35	7	N6	1707							
Bramley, P.S.	M1	7	7	J34	1212							1
Bregazzi, P.K.	C24	28	2	J16	416							1
Brewster, D.J.*	B35	23	7	N12	19							1
Brown, A.M.*	L50	23	7	J13	2442				1			4
Brown, A.M.*	L50	23	7	J13	2443							
Brown, A.M.*	L50	23	7	J13	2444							
Brown, K.	R1	35	7	P21	723			1			1	5
Brown-Grant, K.	O2	33	7	B21	542			1	1	1		5
Brown-Grant, K.	O2	5	7	J14	3077							
Bryant, M.J.	L10	2	7	A12	1084			1	1			5
Bryant, M.J.	R2	5	7	A16	1164							
Buckley, S.K.L.	C1	21	2	A12	393							1
Bull, A.L.*	P9	6	6	B17	2123							1
Burnet, B.	S9	5	3	E9	3060	3	2	1	1	1	1	11
Buse, A.*	B2	21	2	A12	392							1
Bygott, J.D.*	C12	40	8	N2	321							1
Calvert, I.	L68	1	3	J15	1974							1
Campbell, J.I.	G4	9	1	A6	2207		1					2
Chamove, A.S.	S20	7	8	Q1	1224	4	1	1	1	3		13
Chamove, A.S.	S19	13	8	A12	2782							
Chantrey, D.F.*	C12	19	6	J11	982		1		1		1	4
Chapman, C.J.*	A2	23	5	H1	1469	1	2				1	6
Chapman, R.F.	L14	40	3	E2	1398	1	2			2	1	7
Chiney, M.*	P9	5	3	E4	1129							1
Christie, D.W.	M12	5	7	A12	2105							1
Claridge, M.F.	C20	9	3	R6	1284		1			1		3
Clarke, B.	B6	13	1	N2	1783							1
Clarke, M.R.*	P3	38	7	N2	1378							1
Connolly, K.J.	S10	5	3	B9	2058	3	2		2		1	10

Connolly, K.J.	S9	5	3	E9	3060							
Cook, R.	S10	5	3	B9	2058	1	3		1		1	7
Coombes, C.F.B.	A1	9	6	J7	2261							1
Cooper, K.J.	N15	36	7	J34	778							1
Corbet, S.A.	L68	1	3	J15	1974	2						3
Costall, B.	B29	35	7	L4	662	2	2	2	1	3	1	12
Cowan, A.	H7	38	7	E9	1377							1
Cowan, P.	H7	38	7	E9	1377		2	1	3	1		8
Cowey, A.	N13	33	7	B21	541	2	5	2	1	2	2	18
Cowey, A.	07	33	8	N8	597							
Cowey, A.	N13	33	7	B21	1610							
Cowey, A.	L5	35	7	B6	2644							
Cowley, J.J.	L51	33	7	P7	1627				2			4
Cowley, J.J.	B11	1	7	A12	2011							
Cox, T.	N13	35	7	N7	2672	1	3		1			6
Cranford, J.	B27	33	7	J29	90							1
Creese, I.	C8	35	7	B21	2654		3					4
Crighton, D.B.	N15	36	7	J34	778							1
Croll, N.A.	L49	21	2	J30	397			1		1		3
Crook, J.H.	N7	36	6	A12	1760		1	1	1			4
Daly, M.*	B35	6	7	Z1	1186	1		2	1	1	2	8
Davidson, J.M.	02	5	7	J14	3077	1	1	1	2	1	2	9
Davies, J.A.	B7	38	7	J22	3291	4	1			1	1	8
Davies, L.M.	C16	6	8	N2	257							1
Davies, V.J.	C20	1	7	J14	1063	1						2
Dawkins, M.	010	38	1	B9	2338		1		2	1	1	6
Dawkins, R.	010	38	1	B9	2338				3		1	8
Day, S.	L18	14	7	A12	1817							1
Delius, J.D.	D6	23	6	E9	370		2	2	1		4	12
Delius, J.D.	D6	31	6	J13	1566							
Delius, J.D.*	D6	26	6	A12	2539							
Dewson, J.H.	07	33	8	N8	597		1				1	3
Diamond, I.T.	B27	33	7	J29	90		1	3		1		6
Dicker, N.A.	D2	9	3	N13	286							1
Dickinson, A.*	S27	19	7	Q1	1007		5	2	2	2	1	19
Dickinson, A.*	S27	33	7	P7	2594							
Dickinson, A.*	S27	33	7	P7	2596							
Dilks, R.A.	H10	38	7	P7	3294	1						2
Dimond, S.J.	C17	13	6	A12	1791		1					4
Disney, R.H.L.*	M2	12	3	E5	2179		1		1			3
Dixon, A.F.G.	G4	9	3	J3	1266	1	1				1	5
Doncaster, C.C.	H2	12	2	N5	2174						1	2
Drewett, R.F.*	07	5	7	N2	3080	1	2	3	1	1	2	12
Duncan, I.J.H.	E3	2	6	B31	1078		1		1	4	1	11
Duncan, I.J.H.	E3	40	6	A12	1407							
Duncan, I.J.H.	E3	40	6	A12	2397							
Duncan, I.J.H.	E3	40	6	A12	2399							
Dunn, E.K.*	013	13	6	I1	783	1		1				3
Edwards, D.A.	E8	36	7	P7	771	1	1		2	1		6
Emmerton, J.	D6	23	6	E9	370			1			2	4
Ettlinger, G.	S2	19	8	N8	1009	2	2	5	2	4	5	23
Ettlinger, G.	L51	31	8	B21	2537							
Evans, S.M.*	N7	1	6	A12	1997	1			1		1	7
Evans, S.M.*	N7	2	2	A12	2021							

Everitt, B.J.	B19	36	8	D1	2746		3	1	1	6	1	13
Ewbank, R.	L10	2	7	A12	1084	2			1			6
Ewbank, R.	C1	2	7	A12	3037							
Ewbank, R.	C1	7	7	B32	3118							
Ewing, L.S.*	E8	7	3	B9	260	1						3
Ewing, L.S.*	E8	2	3	B9	3028							
Eysenck, H.J.	S20	7	8	Q1	1224			1				3
Fallows, D.J.	O7	35	7	P7	2686							1
Falls, J.B.	C12	1	6	C2	2005			4	3	1	3	13
Falls, J.B.	C12	1	6	C2	2006							
Field, J.E.	B36	7	7	V2	1213							1
File, S.E.	L18	15	7	Q1	825	5	3	2	6	5	5	36
File, S.E.	L18	14	7	A12	1817							
File, S.E.*	L18	15	7	Q1	1833							
File, S.E.*	L18	35	7	P21	2706							
Fletcher, K.E.	H2	9	3	E2	2225							1
Fossey, D.*	C12	1	8	A12	1068		1		1			3
Franklin, K.B.J.	L30	33	7	P7	565	1	1	2	4		1	10
Free, J.B.	H2	5	3	E2	244		1	3			4	13
Free, J.B.	H2	40	3	A12	1395							
Free, J.B.	H2	10	3	A17	2301							
Fulker, D.W.	C17	16	7	J11	1872	1						2
Fullerton, C.	L5	19	6	A12	977	3			1			5
Fuzeau-Braesch, S.	Y2	35	3	R2	1682							1
Gaffan, D.*	L66	33	7	N8	562	1	1			4		8
Galloway, D.*	P9	38	6	B25	1370							1
Games, D.E.	C18	1	3	J21	2992							1
Gatehouse, A.G.	B3	23	3	E2	2421			1				2
Gilbert, A.B.	E3	36	6	A12	1761							2
Gilbert, A.B.	E3	5	6	R2	2100							
Gillett, S.D.	Y2	35	3	R2	1682	2	1		1	1	2	10
Gillett, S.D.*	Y2	7	3	A12	2138							
Gillett, S.D.*	Y2	7	3	A12	2140							
Godden, D.H.*	B37	31	3	J13	48	1		1				4
Godden, D.H.*	B34	28	3	J21	2496							
Gormezano, I.	O6	38	1	B3	3265							1
Goss-Custard, J.*	N11	9	6	N1	1301			2	3	3	1	10
Graham, D.*	G4	40	3	J13	1396				1		2	4
Gray, J.A.	O7	19	7	Q1	1945	3	1	1		2		16
Greenway, A.P.	A3	16	5	B3	839	1		1				3
Greig, F.	O2	5	7	J14	3077							1
Griffiths, M.	N15	36	7	J34	778							1
Guinness, F.	L11	36	7	H3	1773							4
Gush, G.H.	T2	9	6	B25	2268							1
Hall, G.H.	H3	35	7	N2	2666							1
Harlow, H.F.	S20	7	8	Q1	1224							2
Harlow, H.F.	S19	13	8	A12	2782							
Harr, M.B. ter*	O8	28	7	H3	440							1
Harris, M.P.*	O13	9	6	B17	1296				1		1	4
Harrison, C.J.O.*	T3	5	6	I1	2098	2	1		1			5
Hartnoll, R.G.*	I1	40	2	J28	1390					1	2	4
Hassell, M.P.	L48	37	3	J3	1347	1						3
Hawkes, C.*	E1	28	3	A17	419							3

Haynes, N.B.	N15	5	7	P7	2113				1			2
Heise, G.A.	R3	35	7	J11	652			1	1		1	4
Hendrickson, A.*	L51	37	1	P17	304							1
Herberg, L.J.	L30	31	7	A12	475	2	1	6	4			17
Herberg, L.J.	L30	33	7	P7	565							
Herberg, L.J.	L4	35	7	N7	2675							
Herbert, J.	B19	7	8	A12	2157		2		3	1	1	11
Herbert, J.	B19	36	8	D1	2746							
Herbert, J.*	C6	5	8	P7	3097							
Hill, F.W.G.	B36	7	7	V2	1213							1
Hill, R.M.	C6	31	7	E10	57							1
Hillier, J.G.	B7	38	7	J22	3291							1
Hillman, W.S.*	L46	28	3	N2	1541							1
Hinde, R.A.	C16	6	8	N2	257	5	5		8	3	3	29
Hinde, R.A.	C16	36	6	J14	1763							
Hinde, R.A.	C16	5	6	A12	2088							
Hinde, R.A.	C16	5	6	J34	2099							
Holyoak, D.T.*	P9	12	6	B17	2190	1					2	4
Horn, G.	C6	31	7	E10	57	2	3	1			3	15
Horn, G.	C6	30	6	B21	2618							
Huggins, R.J.	B8	9	5	J38	2258							1
Hughes, B.O.	E3	2	6	B31	1078	2	2	2	1	5	3	19
Hughes, B.O.	E3	40	6	A12	2399							
Hughes, B.O.	E3	40	6	A12	2400							
Hughes, B.O.*	E3	36	6	B31	2724							
Ikin, M.	Y2	23	6	N2	372							1
Ison, J.R.	O7	19	7	Q1	1945	5	2	1		3	2	14
Iversen, S.D.	C8	35	7	P21	1739	3	5	4	3	12	10	43
Iversen, S.D.	C8	33	8	B21	2610							
Iversen, S.D.	C8	35	7	B21	2654							
Johnson, F.N.	B24	35	7	D3	1698			1	1			6
Johnson, V.A.	L5	38	6	R2	3282							1
Jolley, A.*	C19	31	8	P19	513	1						2
Jones, B.P.	O7	35	7	P7	2686							1
Jones, R.B.	H10	2	7	P7	3043	5	2		2	4	1	18
Jones, R.B.	H10	38	7	P7	3294							
Joyce, P.F.	E11	16	7	P17	916							1
Kelly, P.H.	O7	26	7	J11	524		4	1	2			8
Kelroe, E.J.	O6	38	1	B3	3265							1
Kennedy, J.M.	C1	23	7	A12	1485							1
Kennedy, J.S.*	L46	40	3	A24	2384	2	1			2	1	7
Kerkut, G.A.	B24	35	3	Q1	615					1		3
Kerkut, G.A.	S17	35	7	C7	645							
Kiley, M.*	S29	1	7	Z1	1065			2		2	1	6
Kleiman, D.G.	L73	6	7	B9	2129	4			1		1	7
Klepal, W.	O1	21	2	J17	396							1
Kumar, R.	L51	35	7	P15	2696					2		5
Land, M.F.*	S29	40	3	N2	3312	1		2				4
Lazarus, J.	N7	36	6	A12	1760		1			1	1	6
Lea, R.G.	R5	23	6	B9	18							1
Leake, L.D.	P6	30	3	C7	1655							1
Leslie, J.	O6	16	7	P20	2852	1				1		4
Lewis, C.T.	B3	23	3	E2	2421							1
Lincoln, G.A.*	L11	2	7	J19	1095		1		1			4

Lincoln, G.A.	L11	36	7	H3	1773							
Lloyd, I.H.	O7	40	6	Q1	2402							1
Logan, M.	G4	9	3	J3	1266							1
Lowe, G.	H9	35	7	P21	721			1				4
Lowe, G.	H9	16	7	A12	877							
Lowe, G.	H8	35	7	P6	2694							
Macauley, E.D.M.*	H2	21	3	E2	403	1						2
Mackie, A.M.*	A8	2	2	S5	2025	1				2		4
Macmillan, A.St C.	O7	19	7	Q1	1945		1	1	2			5
Manning, A.	E8	40	3	A12		1	1	2	3		1	9
Martin, A.	G3	23	3	J21	353			1	1			3
Mayes, A.R.	L5	35	7	B6	2644					1		5
Mayes, A.R.*	L5	35	7	B6	2648							
McClelland, R.J.	L51	33	7	P7	1627							1
McFarland, D.J.	O7	37	1	A14	2322	1	2	1	2	3	2	13
McFarland, D.J.	O7	40	6	Q1	2402							
McLannahan, H.*	L9	11	6	B9	2318							1
Meadows, P.S.	G4	9	1	A6	2207	1	1					3
Meese, G.B.	C1	2	7	A12	3037	1		3	1	1		9
Meese, G.B.	C1	7	7	B32	3118							
Messenger, J.B.	S11	19	2	A12	1918	2						4
Michael, R.P.*	B9	5	8	A3	1170	1		3	3	4	3	16
Michael, R.P.	B9	36	8	R1	1781							
Millenson, J.R.	O6	16	7	P20	2852	1		2		2		7
Millenson, J.R.	O6	38	1	B3	3265							
Miller, G.R.	B1	23	6	J7	1476					1		2
Milner, A.D.	S2	19	8	N8	1009	2				1	2	7
Mishkin, M.	C8	33	8	B21	2620			1	1	4	1	8
Mitchell, D.E.	C10	31	7	N2	1576		1	2	1	3		8
Morris, A.	B33	13	7	L1	1802							1
Morris, P.*	L54	9	7	O2	2289							1
Morrison, C.F.	H3	35	7	N2	2666		2	1				4
Mosher, J.I.*	M9	23	2	P11	3							1
Moss, R.	B1	23	6	J7	1476						1	4
Mugford, R.A.	M11	36	7	H3	757	2	1				1	5
Muntz, W.R.A.	S27	23	5	V3	1474		1				1	4
Murray, R.D.H.	G3	23	3	J21	353							1
Murton, R.K.	A1	9	6	J7	2260						1	3
Murton, R.K.	A1	9	6	J7	2261							
Naylor, E.	C24	28	2	J16	416				4			8
Naylor, E.	I1	28	2	H1	1537							
Naylor, R.J.	B29	35	7	L4	662	2	2	2	1	3	1	12
Neaves, W.B.	M1	7	7	J34	1212							1
Nicolas, G.	Y2	35	3	R2	1682							1
Noble, J.*	L66	33	8	B21	1648							1
Norris, M.L.	C4	2	7	L1	1096							3
Norris, M.L.	C4	2	7	J34	2044							
Northmore, D.P.	S27	23	5	V3	1474		1					2
Nottebohm, F.	C15	36	6	S1	2725							1
Nowell, N.W.	N11	36	7	H3	757	6	4	1	2	1	1	19
Nowell, N.W.	H10	2	7	P7	3043							
Nowell, N.W.	H10	38	7	P7	3294							
Oakley, D.A.	L67	33	7	P7	95		3	1	2	2	3	17

Oatley, K.	S27	31	7	J11	1572							1
Oliver, G.W.O.	B24	35	3	Q1	615							2
Ollason, J.C.	S28	12	6	B9	1251						2	4
Ollason, J.C.	S28	28	6	A12	1547							
Osborne, R.H.	S17	35	7	C7	645							1
Outram, G.W.*	E2	33	7	J12	546							1
Owen, M.*	S12	9	6	I1	3213			1		1	1	5
Parker, A.H.*	L20	12	3	B34	272							1
Parsons, J.*	C26	5	6	I1	1157						1	2
Patterson, D.J.*	B37	15	2	B9	2790							1
Payne, A.P.	B19	2	7	B9	235	2	2	1	2	1	1	14
Payne, A.P.	B19	36	7	J14	752							
Payne, A.P.	B19	36	7	N2	769							
Payne, A.P.	B19	36	7	A12	1765							
Peal, R.E.F.*	P9	12	6	B25	2193							1
Penny, R.H.C.	B36	7	7	V2	1213	1	2					4
Pfaff, D.W.	C15	36	6	S1	2725							1
Plush, J.T.	B36	7	7	V2	1213							1
Pollard, D.G.*	B30	9	3	B34	3179							1
Pond, C.M.*	O11	31	3	J13	47	1	1		1			4
Poole, T.B.*	A11	2	7	J38	3050	3	4	3	1	2		14
Porter, R.H.	L5	19	6	A12	977	6	2	3	2	3	3	21
Porter, R.H.	L5	38	6	R2	3282							
Potter, I.C.	B8	9	5	J38	2258							1
Potts, G.W.*	P3	9	5	M4	2256		1					2
Priestnall, R.*	S10	6	7	A12	1178		1			1		4
Priestnall, R.*	S10	6	7	A12	3103							
Prior, R.N.B.*	H1	12	3	E5	2178							1
Purvis, K.	N15	5	7	P7	2113							1
Pye, J.G.	L30	31	7	A12	475							1
Raisman, G.	O2	33	7	B21	542					1		3
Ravizza, R.	B27	33	7	J29	90							1
Redfern, P.H.	B7	38	7	J22	3291	4	1		1			8
Remington, R.E.	E13	16	6	B29	845	1						2
Reynolds, W.J.	C20	9	3	R6	1284					1		2
Rick, J.T.	B24	35	3	Q1	615	1			1			3
Ridley, R.M.	L51	31	8	B21	2537		2	1	1	2	4	14
Robbins, T.G.W.	C8	35	7	P21	1739	1	1		5	3	2	15
Rogers, D.J.	L48	37	3	J3	1347	1					1	3
Rolls, B.J.	O7	35	7	P7	2686	3	1	1	1	3		10
Rolls, E.T.*	O7	26	7	B21	520	6	2	4	6	2	2	26
Rolls, E.T.	O7	26	7	J11	524							
Rolls, E.T.*	O7	31	7	J11	1570							
Rose, S.P.R.	C6	30	6	B21	2618	2	4					8
Rosenblum, L.A.	S19	13	8	A12	2782							1
Rowland, C.G.	E3	40	6	R2	3323							1
Russell, I.S.	L67	33	7	P7	95	1	2	1	1	2	2	13
Russell, I.S.	L18	15	7	Q1	825							
Russell, P.A.	H9	13	7	B29	788	1		1		2		9
Russell, P.A.*	A6	14	7	A12	1818							
Russell, P.A.	A6	14	7	A12	1819							
Sage, B.L.*	P9	12	6	B25	2192							1
Sales, G.D.*	L50	1	7	J38	1066			1		1	1	5
Sales, G.D.*	L50	2	7	A12	1085							

Sanders, J.D.	S11	19	2	A12	1918		1					2
Savage, R.M.*	P9	5	4	N2	1143							1
Scruton, D.M.	B19	7	8	A12	2157			1			1	3
Scruton, P.	B24	16	7	J36	1884	2						3
Service, M.W.*	A1	7	3	E5	1194							1
Seymour, M.K.	H2	12	2	N5	2174						1	2
Sharpe, R.M.	B33	13	7	L1	1802		1					2
Sheldon, M.H.*	N6	16	1	Q1	1836							1
Short, R.V.	L11	36	7	H3	1773	1					1	3
Sibly, R.M.	O7	37	1	A12	2322		2	1		1	2	7
Siddle, D.A.T.*	S18	15	8	B29	169			1		1		3
Simmons, K.E.L.*	P9	11	6	B25	2319			2				5
Simmons, K.E.L.	L5	5	6	J38	3075							
Slater, P.J.B.	S28	12	6	B9	1251	1	2			1	4	12
Slater, P.J.B.	S28	28	6	A12	1547							
Smith, D.A.*	E7	40	8	J11	3338	1		1			1	4
Smith, G.A.*	H5	12	6	A25	1250			1	1			3
Smith, J.C.*	L50	1	7	J38	1067		3	2	1	1	1	9
Smith, J.M.	L49	21	2	J30	397		1	2				5
Soane, I.D.	B6	13	1	N2	1783							1
Spencer, R.	T2	9	6	B25	2268						1	3
Staddon, B.W.	C18	1	3	J21	2992							1
Stechler, G.	C6	31	7	E10	57							1
Steel, E.	C16	36	6	J14	1763	1	1		3		1	11
Steel, E.	C16	5	6	A12	2088							
Steel, E.	C16	5	6	J34	2099							
Stefanski, R.A.	C12	1	6	C2	2005							2
Stefanski, R.A.	C12	1	6	C2	2006							
Stephens, D.B.	C1	16	7	P7	2890	1	3				1	6
Stevens, R.	N13	33	7	B21	541	2	1	1		1		8
Stevens, R.	N13	33	7	B21	1610							
Stevens, R.*	N13	33	7	P6	2603							
Stevenson-Hinde, J.*	C12	13	6	A12	1792			1	2			5
Stolerman, I.P.	L51	35	7	P15	2696	1		2	1	4	2	12
Stride, G.O.	G3	23	3	J21	353							1
Strongman, K.T.	E11	40	7	P17	320	2	1					6
Strongman, K.T.	E13	16	6	B29	845							
Strongman, K.T.	E11	16	7	P17	916							
Sudd, J.H.*	H10	7	3	A12	2139							1
Swanson, H.H.	B19	2	7	B9	235	1	2	1		2	2	12
Swanson, H.H.	B19	36	7	J14	752							
Swanson, H.H.	B19	36	7	N2	769							
Swanson, H.H.	B19	36	7	A12	1765							
Sweller, J.*	P9	19	7	Q1	1944							1
Tait, R.W.	O6	38	1	B3	3265		1					2
Taylor, I.B.	P6	30	3	C7	1655							1
Thearle, R.J.P.	A1	9	6	J7	2260							2
Thearle, R.J.P.	A1	9	6	J7	2261							
Thompson, G.	D6	23	6	E9	370							1
Thompson, J.	A1	9	6	J7	2260							1
Thompson, M.L.	E8	36	7	P7	771				2			3
Thorpe, W.H.*	C12	1	6	B11	221	2			1			11
Thorpe, W.H.*	C12	1	6	B11	222							

Thorpe, W.H.*	C12	1	6	B11	223							
Thorpe, W.H.*	C12	1	6	B11	224							
Thorpe, W.H.*	C12	1	6	B11	225							
Thorpe, W.H.*	C12	1	6	B11	226							
Thorpe, W.H.*	C12	1	6	B11	227							
Thorpe, W.H.*	C12	1	6	B11	228							
Thorson, J.	P9	31	6	J13	1565							1
Toates, F.M.	S27	31	7	J11	1572		2			4	1	12
Tomkins, T.	R2	5	7	A16	1164				1			2
Treisman, M.*	O7	38	1	P14	3270			4		1	1	8
Turner, J.R.G.	R5	23	6	B9	18			2				4
Turner, J.R.G.	Y2	23	6	N2	372							
Tye, N.C.	N13	35	7	N7	2672	1	1	1	1	1		7
Tyler, S.J.*	C12	7	7	A13	2151							4
Vane-Wright, R.*	L13	5	3	N2	1137							1
Verbeek, N.A.M.*	O12	12	6	J2	277							1
Vernon, J.D.R.*	P9	9	6	B17	2266							1
Vollrath, F.W.	D6	31	6	J13	1566						1	2
Wainwright, A.	C12	19	6	B9	978							1
Walker, I.*	L49	15	2	A12	809							1
Warburton, D.M.	R3	35	7	J11	652		1					3
Warburton, D.M.	R1	35	7	P21	723							
Ward, P.*	L14	7	6	I1	1200						1	2
Warren, E.W.*	L33	9	5	J20	3205	2	1		1			5
Waterhouse, F.L.	D2	9	3	N13	286							1
Weidmann, U.	L5	5	6	J38	3075							1
Weihs, D.*	C7	7	5	N2	2145							1
Weiskrantz, L.*	O7	33	8	R9	1653		5	3		1		10
Wells, J.	C1	5	2	A12	1112							1
Wells, M.J.	C1	21	2	A12	393		1					3
Wells, M.J.	C1	5	2	A12	1112							
Whitfield, I.C.	B27	33	7	J29	90					1		2
Wilcock, J.	C17	16	7	J11	1872							3
Wilcock, J.*	B24	10	1	A11	2299							
Wilcock, J.*	B24	11	7	A12	2321							
Williams, D.I.	H9	35	7	P21	721	1	3		1	1		13
Williams, D.I.	H9	13	7	B29	788							
Williams, D.I.*	H9	14	7	Q1	807							
Williams, D.I.	H9	16	7	A2	877							
Williams, D.I.*	H9	19	6	B29	980							
Williams, D.I.	A6	14	7	A12	1819							
Williams, D.I.	H8	35	7	P6	2694							
Williams, I.H.	H2	5	3	E2	244		1	2		1	2	9
Williams, I.H.	H2	40	3	A12	1395							
Williams, I.H.	H2	10	3	A17	2301							
Wilson, M.I.	B9	5	6	A12	1151					1	1	3
Wilton, R.N.*	D3	16	1	L3	827							1
Wise, D.R.	B11	1	7	A12	2011							1
Wood-Gush, D.G.M.*	E3	10	6	A12	1317	1	3	3	1	3	4	22
Wood-Gush, D.G.M.	E3	40	6	A12	1407							
Wood-Gush, D.G.M.	E3	36	6	A12	1761							

Wood-Gush, D.G.M.	E3	5	6	R2	2100							
Wood-Gush, D.G.M.	E3	40	6	A12	2397							
Wood-Gush, D.G.M.	E3	40	6	A12	2400							
Wood-Gush, D.G.M.	E3	40	6	R2	3323							
Wookey, J.A.	E11	40	7	P17	320							1
Wookey, P.E.	E11	40	7	P17	320	2	1		1	1		8
Wookey, P.E.	E11	16	7	P17	916							
Wray, S.R.*	H9	35	7	P21	124	2		1		1		5
Wyatt, A.C.	B33	13	7	L1	1802							1
Yates, J.O.	C1	38	7	P7	1382				1			2
Yeo, P.F.*	C5	40	3	J28	1401							1
Zigmond, R.E.	C15	36	6	S1	2725							1
Zucker, R.S.*	L61	31	2	J29	452							3
Zucker, R.S.*	L61	31	2	J29	453							
Zucker, R.S.*	L61	31	2	J29	454							

APPENDIX V

Individual papers on animal behaviour recorded in Animal Behaviour Abstracts, Volumes 2 (1974) to 7 (1979), by authors who generated at least 10 abstracts between 1973 (Behavioural Biology Abstracts, Volume 1) and 1980 (Animal Behaviour Abstracts, Volume 8) overall, with details of: a. Author's name b. Volume and date of Animal Behaviour Abstracts c. Work base d. Field of interest e. Animals used f. Journal in which paper published, and g. Abstract reference number.

Notes:
i) Keys to the four coded categories (c-f) are supplied below (pp. 318-344).
ii) The linking of partners in authorship can be made via the abstract reference number.
iii) Some authors were foreign visitors, but all work recorded here was carried out in the U.K. or its waters.
iv) Changes of name through marriage have not been identified or indicated.

a	b	c	d	e	f	g
Andrew, R.J.	2/74	S28	26	6	B20	1134
	2/74	S28	26	6	B20	2033
	3/75	S28	36	6	A12	2286
	3/75	S28	36	6	A12	2287
	3/75	S28	1	6	A12	2680
	3/75	S28	37	1	B9	2972
	4/76	S28	33	6	B20	213
	4/76	S28	33	6	B20	214
	5/77	S29	5	6	J11	858
	5/77	S28	36	6	H3	3735
	7/79	S28	36	6	B9	3791
	7/79	S28	1	8	N12	4451
Archer, J.	2/74	S28	36	6	A12	3055
	2/74	S28	40	7	A15	3836
	3/75	S28	36	6	A12	399
	3/75	S28	36	6	B6	402
	3/75	S28	36	7	A12	3427
	4/76	S28	40	7	B6	1159
	4/76	S28	10	7	B2	2057
	4/76	S28	2	7	B6	2911
	5/77	P8	36	6	P7	397
	5/77	P8	36	6	P7	1579
	5/77	S28	36	6	H3	3735
	5/77	P8	10	7	B29	4481
	5/77	P8	36	7	A12	3762

Baker, R.	4/76	S16	1	3	S5	1758
	4/76	S16	1	3	N2	2840
	6/78	S16	21	2	B6	3074
	7/79	S16	5	3	E1	725
	7/79	S16	1	3	J21	2586
	7/79	S14	1	3	P5	4375
	7/79	S14	1	3	P5	4376
	7/79	S14	1	3	P5	4377
	7/79	S14	2	3	B18	4482
Baldwin, B.A.	2/74	C1	25	7	A12	1949
	3/75	C1	27	7	P7	147
	4/76	C1	8	7	J33	1711
	4/76	C1	1	7	P7	1798
	4/76	C1	2	7	A20	1849
	4/76	C1	6	7	A20	1926
	4/76	C1	8	7	P4	2809
	5/77	C1	27	7	P7	1323
	5/77	C1	8	7	J33	3008
	5/77	C1	25	7	A20	3418
	5/77	C1	33	7	A20	3597
	5/77	C1	17	7	A12	3895
	6/78	C1	38	7	P7	626
	6/78	C1	25	7	P7	698
	7/79	C1	27	7	P7	3375
	7/79	C1	33	7	A20	3534
Bateson, P.P.G.	2/74	C6	30	1	S1	220
	2/74	C12	30	6	S1	224
	2/74	C12	19	6	A12	1478
	2/74	C12	19	6	J11	3297
	3/75	C12	30	1	B13	271
	3/75	M15	30	6	B13	278
	3/75	C12	19	6	N2	1496
	3/75	C12	19	6	A12	1509
	3/75	C12	30	6	B21	2180
	3/75	C12	13	6	B9	3444
	3/75	M15	30	6	B21	3307
	4/76	C12	13	6	A12	3658
	7/79	C12	13	7	B9	356
	7/79	C12	18	6	B6	417
	7/79	C11	30	6	B21	3571
Blackman, D.E.	2/74	B24	18	7	A15	1453
	2/74	B24	17	7	J36	2248
	3/75	B24	17	7	P21	531
	4/76	B24	17	7	Q1	439
	4/76	B24	35	6	J31	1410
	4/76	B24	17	7	J31	1556
	4/76	B24	17	7	P21	2607
	4/76	B24	18	7	P17	2644
	4/76	B24	17	7	P16	3718
	5/77	B24	17	7	B6	523
	5/77	B24	18	7	P22	552

	5/77	B24	17	7	P4	1679
	5/77	B24	18	7	J36	2889
	5/77	B24	17	6	J36	3855
	5/77	B24	17	7	J36	3888
	7/79	C19	38	7	P17	3058
Blakemore, C.	2/74	C10	31	7	N2	2023
	2/74	C10	31	7	E10	2853
	3/75	C10	13	7	E10	2321
	4/76	C10	24	7	E10	3238
	5/77	C10	31	7	J33	1378
	5/77	C10	24	7	E10	3373
	6/78	C10	31	7	E10	806
	6/78	C10	31	7	E10	3239
	7/79	C10	30	8	B21	1274
Boakes, R.A.	2/74	S27	17	6	J36	1380
	2/74	S27	19	6	J36	2289
	3/75	S27	17	1	J36	3524
	3/75	S27	17	7	J11	3571
	3/75	S27	19	6	J36	3720
	5/77	S27	19	6	J36	594
	6/78	S27	1	6	Q1	1321
	6/78	S27	17	7	J36	3725
Booth, D.A.	2/74	B24	18	7	J11	511
	2/74	B24	31	7	P7	1117
	2/74	B24	18	7	Q1	2264
	2/74	B24	17	7	P7	3202
	3/75	B24	18	7	P4	576
	3/75	B24	8	7	B6	691
	3/75	B18	37	7	P20	1857
	3/75	B24	18	7	P6	2456
	3/75	B24	8	7	P21	2607
	3/75	B24	8	7	P6	2622
	3/75	B24	8	7	P6	2624
	3/75	P8	37	7	N2	2981
	4/76	B24	27	7	B6	1299
	4/76	B24	8	7	P7	1722
	4/76	B24	27	7	P7	2310
	6/78	B24	27	7	P24	1823
	6/78	B26	35	7	B21	2095
	6/78	B26	18	7	P4	2280
	6/78	B24	18	7	B29	2289
	7/79	B24	27	1	N14	2013
Brain, P.F.	2/74	S31	2	7	B9	3542
	3/75	S31	13	7	L4	2326
	4/76	S31	2	7	P7	749
	5/77	B20	36	7	J14	414
	5/77	S31	36	7	J14	2761
	6/78	S31	36	7	P4	2157
	6/78	S31	7	7	P7	4400
	7/79	S31	31	7	L4	3415

	7/79	B23	36	7	P7	343
	7/79	S31	36	7	J14	1332
	7/79	S31	2	7	A8	1586
	7/79	S31	2	7	A12	1588
	7/79	S31	6	7	P7	2767
	7/79	S30	36	7	P6	3795
	7/79	S31	2	7	P7	4510
	7/79	S31	2	7	P7	4511
Broom,D.M.	3/75	R4	7	2	M4	2814
	5/77	R4	8	6	C8	697
	5/77	R4	8	6	B17	2980
	6/78	R4	1	7	J38	2530
	6/78	B12	13	7	A12	3629
	6/78	R6	8	7	A11	4015
	7/79	R4	13	7	A12	2246
Burnet, B.	2/74	S9	10	3	S1	848
	2/74	S9	5	3	J21	1657
	2/74	S10	5	3	B9	1675
	3/75	S9	10	3	B2	1812
	3/75	H9	10	3	G3	2926
	4/76	H9	30	3	B6	1384
	5/77	S9	1	3	A12	4136
	5/77	S9	10	3	G3	2281
	6/78	S9	5	3	B2	1398
	7/79	S9	10	3	A12	2980
Chamove, A.S.	2/74	S20	13	8	B9	407
	2/74	S20	18	8	J11	533
	2/74	S20	7	8	F2	795
	2/74	S20	13	8	J24	1353
	3/75	S19	38	8	P9	1063
	4/76	S20	19	8	J6	552
	5/77	S20	2	8	F2	823
	6/78	S20	36	8	A8	3603
	6/78	S20	19	8	J26	3838
	6/78	S20	6	8	C4	4359
Chance, M.R.A.	2/74	B17	38	8	L1	3823
	3/75	B17	6	8	F2	4028
	4/76	B23	35	7	P21	322
	4/76	B23	35	7	P21	2456
	4/76	B23	35	7	P21	2503
	4/76	B23	35	7	N7	2507
	5/77	B17	N/A	8	B18	1158
	5/77	B17	6	8	F2	4332
	7/79	B17	7	8	B18	2833
	7/79	B17	1	8	B12	4464
Connolly, K.	2/74	S10	10	3	S1	848
	2/74	S10	5	3	J21	1657
	2/74	S10	5	3	B9	1675
	3/75	S10	10	3	B2	1812

	3/75	S10	10	3	G3	2926
	5/77	S10	10	3	G3	2281
	5/77	S10	1	3	A12	4136
	7/79	S10	10	3	A12	2980
Cooper, S.J.	2/74	07	31	7	B21	1126
	2/74	07	26	7	P7	2866
	2/74	07	26	7	E11	2870
	2/74	B11	26	7	E10	2889
	4/76	B11	19	11	B28	1636
	5/77	B11	35	7	P22	1543
	7/77	B11	15	7	B28	381
	7/79	B11	35	7	B28	1306
	7/79	B11	35	7	P22	2143
	7/79	S27	35	7	P22	3658
Costall, B.	2/74	B29	35	7	N4	266
	2/74	B29	35	7	E7	1209
	3/75	B29	35	7	E7	2218
	3/75	B29	35	7	E7	3368
	4/76	B29	35	7	E7	267
	4/76	B29	35	7	E7	3597
	5/77	B29	33	7	B21	2670
	6/78	B29	35	7	J32	167
	6/78	B29	35	7	E7	2008
	6/78	B29	35	7	E7	3482
	7/79	B29	35	1	J25	249
Cowey, A.	2/74	07	33	7	E10	1173
	2/74	07	33	7	B21	2903
	3/75	N13	33	7	Q1	1240
	3/75	07	38	8	Q1	1882
	3/75	07	24	8	Q1	1917
	3/75	07	19	8	N8	2517
	3/75	07	24	8	P2	3064
	4/76	07	19	8	N8	555
	4/76	07	33	8	N8	3499
	5/77	07	33	7	B21	2667
	6/78	07	24	7	P7	1681
	6/78	07	33	8	B19	3370
	7/79	07	33	7	E10	3537
Cutler, M.G.	4/76	B23	35	7	P21	322
	4/76	B23	35	7	P21	2456
	4/76	B23	35	7	P21	2460
	4/76	G1	35	7	P21	2503
	4/76	G1	35	7	N7	2507
	5/77	G1	7	7	N7	943
	6/78	G1	35	7	P22	165
	7/79	G1	35	7	P22	3689
	7/79	G1	35	7	P22	3704
Dickinson, A.	3/75	S27	18	7	A15	1462
	3/75	S27	33	7	J11	2159

	3/75	S27	33	7	P6	3278
	3/75	S27	17	7	J11	3603
	3/75	S27	18	7	J18	3686
	4/76	S27	18	7	P6	464
	4/76	S27	18	7	L3	3759
	5/77	S27	18	7	A15	2876
	5/77	S27	18	7	Q1	2885
	6/78	C8	27	1	P14	81
	6/78	S27	17	1	A19	3707
	7/79	C8	17	7	J18	4012
Drewett, R.F.	2/74	B32	36	7	A12	1276
	3/75	D6	27	7	Q1	139
	3/75	D6	8	7	A12	1604
	4/76	D6	26	7	P7	203
	4/76	D6	36	7	A12	1471
	4/76	D6	38	7	P7	2117
	5/77	D6	27	7	P7	1319
	6/78	D6	36	7	P7	2142
	7/79	D6	27	7	J18	2023
	7/79	D6	8	7	A12	2548
Duncan, I.J.H.	3/75	E3	35	6	A20	3326
	5/77	E3	12	6	A20	2207
	6/78	E3	38	6	A20	1635
	6/78	E3	8	6	A20	2437
	6/78	E3	5	6	A20	2646
	6/78	E3	40	6	A20	2918
	7/79	E3	7	6	B16	810
Einon, D.F.	4/76	C8	13	7	P7	2566
	4/76	C8	13	7	A12	3676
	4/76	C8	13	7	Q1	1492
	5/77	C8	13	7	P7	2792
	5/77	C8	13	7	P7	479
	5/77	C8	15	7	Q1	1637
	6/78	C8	13	7	D2	1057
	6/78	C8	13	7	Q1	2222
	6/78	D6	13	7	D2	3668
	7/79	D6	13	7	B6	360
	7/79	D6	13	7	P22	3898
Ettlinger, G.	2/74	L51	19	8	N8	574
	2/74	L51	19	8	N8	1502
	3/75	L51	19	8	N8	2515
	3/75	L51	19	8	N8	2516
	4/76	L51	33	8	B21	237
	4/76	L51	33	8	E11	2417
	4/76	L51	19	8	N2	3846
	4/76	L51	19	8	B21	3848
	4/76	L51	38	8	N8	4525
	5/77	L51	33	8	N8	269
	5/77	L51	31	8	E10	3534
	6/78	L51	19	8	N8	334

	6/78	L51	19	8	P20	336
	6/78	L51	19	8	E10	3836
	6/78	L51	19	8	N8	3837
	7/79	L51	19	8	B18	1426
	7/79	L51	19	8	B18	2436
	7/79	L51	19	8	B18	2437
	7/79	L51	1	8	J11	2664
	7/79	L51	19	8	N8	4131
Everitt, B.J.	3/75	C6	36	8	B21	2307
	3/75	C6	5	7	E7	2783
	3/75	C6	5	8	B21	2797
	4/76	C6	36	7	J11	1468
	5/77	C6	36	7	N2	2136
	6/78	C6	5	7	N11	505
	6/78	C6	5	7	N11	506
	6/78	C6	35	7	P4	952
	6/78	C6	35	7	N2	955
	6/78	C6	36	8	P7	1022
	6/78	C6	35	7	B21	2089
	7/79	C6	5	8	B18	2758
File, S.E.	2/74	L18	35	7	P21	324
	2/74	L18	15	7	A12	415
	2/74	L18	35	7	B28	1237
	2/74	L18	35	7	Q1	2138
	2/74	L18	15	7	P6	3147
	3/75	L18	35	7	P21	328
	3/75	L18	6	7	A15	864
	3/75	L18	15	7	D2	3507
	4/76	L56	15	7	P4	2589
	4/76	L56	15	7	B28	3687
	5/77	L56	15	7	D2	489
	5/77	L56	15	7	P4	493
	5/77	L56	25	7	B6	2490
	5/77	L56	35	7	P6	2737
	5/77	L56	15	7	P4	3834
	5/77	L56	15	7	P4	3835
	6/78	L56	35	7	B21	939
	6/78	L56	35	7	P4	953
	6/78	L56	36	7	J32	2179
	6/78	L56	6	7	B28	2691
	6/78	L56	13	7	D2	3646
	7/79	L56	15	7	P4	1368
	7/79	L56	13	7	D2	2241
	7/79	L56	13	7	D2	2251
	7/79	L56	35	7	B28	3740
	7/79	L56	36	7	P73	3808
Free, J.B.	3/75	H2	7	3	A12	4032
	4/76	H2	8	3	B1	1680
	4/76	H2	8	3	A20	3890
	7/79	H2	5	3	B1	721
	7/79	H2	8	3	A20	4210

	7/79	D4	1	3	J5	4361
	7/79	H2	9	3	J7	4876
Gentle, M.J.	2/74	E3	25	6	S5	2719
	3/75	E3	27	6	P7	136
	4/76	E3	25	6	P7	54
	4/76	E3	38	6	B31	4503
	5/77	E3	25	6	C3	50
	7/79	E3	33	6	B12	1245
	7/79	E3	33	6	A12	2084
	7/79	E3	33	6	B12	2086
Gillett, S.D.	2/74	Y2	13	3	A12	374
	2/74	Y2	7	3	A2	3642
	3/75	Y2	7	3	A12	4031
	5/77	Y2	7	2	A2	3142
	6/78	Y2	8	1	A12	2363
	7/79	Y2	9	3	A2	2920
	7/79	Y2	11	3	A12	5080
Goss-Custard, J.	4/76	B35	7	1	A12	4206
	4/76	N9	38	6	A12	4509
	5/77	N9	11	6	E8	2315
	5/77	W1	8	6	A12	2987
	5/77	W1	8	6	J3	4077
	6/78	W1	8	6	J3	2416
	6/78	W1	8	6	J7	2432
	6/78	W1	8	6	J7	3964
	7/79	W1	8	6	I1	1497
Goudie, A.J.	2/74	B4	35	7	P21	308
	2/74	B4	35	7	P21	2135
	2/74	B4	35	7	P21	2136
	3/75	B4	35	7	P21	347
	3/75	B4	35	7	P21	2252
	4/76	B4	35	7	P8	311
	4/76	L8	15	7	L4	1514
	4/76	L8	18	7	P4	2668
	4/76	L8	18	7	P4	3791
	6/78	L8	19	7	P4	325
	7/79	L8	18	7	P4	429
	7/79	L8	18	7	P4	4058
Gray, J.A.	2/74	O7	35	7	P21	1227
	2/74	O7	35	7	P21	3040
	2/74	O7	36	7	P7	3091
	3/75	O7	18	7	A12	1483
	4/76	D6	36	7	A12	1471
	6/78	O7	36	7	P7	2142
	6/78	O7	36	7	P7	2145
Green, A.R.	3/75	O5	35	7	N2	1289
	3/75	O5	35	7	N7	3343
	4/76	O5	35	7	N7	1424

	4/76	05	35	7	N7	3574
	4/76	05	35	7	B28	3611
	4/76	05	35	7	N2	3612
	5/77	05	35	7	N2	304
	5/77	05	35	7	B28	3662
	6/78	05	30	7	B28	3408
	6/78	05	35	7	N7	3493
	7/79	05	35	7	B28	1314
	7/79	05	35	7	B28	1315
	7/79	05	35	7	N7	3619
Hall, G.	2/74	S27	19	7	Q1	2295
	3/75	S27	19	6	Q1	590
	3/75	S27	19	6	J11	1501
	3/75	S27	19	7	J11	1514
	4/76	S27	19	7	A15	532
	4/76	Y3	19	6	Q1	3813
	5/77	Y3	19	1	L3	3961
	6/78	Y3	19	6	Q1	3817
	7/79	Y3	17	7	L3	403
	7/79	Y3	19	7	Q1	458
	7/79	Y3	17	7	J18	2317
Harzem, P.	3/75	B4	17	7	J36	3582
	3/75	B4	17	7	P16	3613
	4/76	B4	17	7	Q1	1537
	4/76	B4	17	7	J36	1546
	4/76	B4	17	7	P16	3719
	5/77	B4	17	7	J36	524
	6/78	B4	17	1	J36	2237
	6/78	B4	17	1	Q1	3708
	7/79	B4	17	1	J36	2315
Herberg, L.J.	2/74	L4	27	7	P7	93
	2/74	L30	38	7	P7	904
	3/75	L30	27	7	J11	145
	4/76	L30	26	7	P4	194
	4/76	L30	26	7	P7	203
	4/76	L30	26	7	B21	206
	4/76	L30	26	7	B21	211
	4/76	L30	27	7	P4	3402
	4/76	L30	26	7	P4	3465
	5/77	L30	35	7	N7	305
	5/77	L30	26	7	B18	2635
	5/77	L30	26	7	B18	2636
	5/77	L30	27	7	J11	3492
Herbert, J.	3/75	C6	36	8	B21	2307
	3/75	C6	5	8	B21	2797
	5/77	C6	5	8	N2	2136
	5/77	L73	36	8	H3	3780
	5/77	L73	36	8	P7	3782
	6/78	C6	36	8	P7	1022

Hinde, R.A.	2/74	C12	15	7	B9	418
	2/74	C12	5	6	J38	749
	2/74	C16	5	6	J38	750
	2/74	C16	36	6	J14	1275
	2/74	C16	6	8	J11	3630
	3/75	C16	38	8	P9	1057
	3/75	C16	36	6	J34	1339
	3/75	C16	5	6	J38	2782
	3/75	C16	24	6	J14	3052
	3/75	C16	6	8	A12	4027
	5/77	C16	36	6	H3	1576
	5/77	C16	5	6	J34	4282
	5/77	C16	7	8	J34	4365
	6/78	C16	6	8	P15	522
	6/78	C16	38	1	B9	612
	7/79	C16	6	8	J10	792
	7/79	C16	7	8	B18	2836
	7/79	C16	5	6	A7	4633
Horn, G.	2/74	C6	30	1	S1	220
	2/74	C6	30	6	S1	224
	3/75	C6	31	7	E10	170
	3/75	C6	31	7	B21	185
	3/75	C12	30	6	B21	218
	4/76	B32	31	1	B18	2312
	7/79	L30	31	6	B21	2035
	7/79	B32	31	8	J33	3451
	7/79	C11	30	6	B21	3571
Howse, P.E.	2/74	S15	18	6	A12	491
	3/75	S15	1	6	A12	740
	4/76	S15	1	3	S5	1758
	4/76	S15	1	6	Z1	1776
	4/76	S15	2	3	S5	1819
	4/76	S15	25	6	N2	2198
	4/76	S16	1	3	N2	2840
	4/76	S15	25	3	J21	3270
	7/79	S14	8	3	A12	2483
	7/79	S14	1	3	J21	2586
	7/79	S14	1	3	P5	4375
	7/79	S14	1	3	P5	4376
	7/79	S14	1	3	P5	4377
	7/79	S14	2	3	B18	4482
Hughes, B.O.	2/74	E3	13	6	B32	2177
	2/74	E3	7	6	A12	3650
	3/75	E3	9	6	B31	953
	3/75	E3	12	6	A20	3941
	4/76	E3	9	6	B32	3089
	4/76	E3	9	6	A20	4363
	5/77	E3	7	6	B31	3154
	6/78	E3	2	6	A12	1356
	6/78	E3	7	6	B31	1463
	6/78	E3	9	6	B31	1538

	6/78	E3	40	6	B31	2914
	6/78	E3	2	6	A20	4167
	7/79	E3	2	6	A20	2678
	7/79	E3	40	6	A20	5218
Iversen, S.D.	2/74	C8	33	8	B21	2061
	2/74	C8	35	7	N3	2141
	2/74	C8	17	7	N2	3210
	3/75	C8	19	8	B21	619
	3/75	C8	13	7	B21	2319
	3/75	C8	33	7	N7	3275
	4/76	C8	35	7	B21	291
	4/76	C8	24	6	P21	1170
	4/76	C8	24	8	J36	1185
	4/76	C8	19	8	N2	1646
	5/77	C8	17	7	S1	1688
	5/77	S5	38	7	A15	3293
	5/77	C8	35	6	P22	3645
	6/78	C8	13	7	A15	252
	6/78	C8	19	7	B21	329
	6/78	C8	33	7	N7	869
	6/78	C8	35	7	N2	955
	6/78	C8	15	7	J11	1084
	6/78	C8	15	7	P4	2232
	6/78	C8	19	8	J36	2338
	6/78	C8	26	7	B21	3284
	6/78	C8	33	8	B21	3367
	6/78	C8	35	7	B21	3456
	6/78	C8	35	7	B28	3514
	6/78	C8	35	7	B21	3522
	7/79	C8	15	7	P7	379
	7/79	C8	20	6	P22	4139
	7/79	C8	33	8	N8	220
	7/79	C8	33	8	B21	2101
	7/79	C8	33	8	B18	2103
	7/79	C8	35	6	P22	2122
	7/79	C8	35	7	B21	2190
	7/79	C8	19	8	B18	2441
	7/79	C8	33	8	N8	3562
	7/79	C8	15	7	P7	3959
Jones, R.B.	2/74	H10	1	7	P7	1621
	2/74	H10	1	7	A12	1622
	2/74	H10	2	7	A15	1643
	2/74	H10	1	7	A12	2400
	2/74	H10	1	7	P7	3507
	3/75	H10	1	7	A15	749
	3/75	H10	25	7	B6	1954
	5/77	E3	25	7	C3	59
	5/77	E3	1	7	B6	4163
	6/78	H10	1	7	B6	422
	6/78	E3	10	6	A20	1562
	6/78	E3	15	6	B12	2229

	6/78	E3	24	6	B12	2973
	7/79	E3	40	6	B31	3094
Keverne, E.B.	5/77	C6	1	8	H3	2002
	5/77	C6	5	8	N2	2136
	5/77	C6	5	8	A7	3119
	6/78	C6	36	8	P7	1022
	7/79	C6	7	8	A12	1724
	7/79	C6	36	8	N2	2220
	7/79	C6	7	8	B18	2853
	7/79	C6	31	1	B18	3407
Krebs, J.R.	3/75	010	8	6	A12	1578
	3/75	B3	7	6	B9	2827
	5/77	012	1	6	B8	763
	5/77	012	8	6	A12	2988
	5/77	012	1	6	A12	4160
	6/78	013	8	6	A22	2418
	7/79	012	8	6	N2	542
Mackintosh, J.H.	2/74	B23	2	7	A12	703
	3/75	B23	1	7	A12	3910
	4/76	B23	35	7	P21	322
	4/76	B23	35	7	P21	2456
	4/76	B23	35	7	P21	2460
	4/76	B23	35	7	P21	2503
	4/76	B23	35	7	N7	2507
	4/76	B23	36	7	J14	2763
	6/78	B23	38	7	L2	636
	6/78	B23	1	7	P7	4113
Mackintosh, N.J.	2/74	S27	17	7	A15	1421
	2/74	S27	18	7	C1	3262
	3/75	S27	19	6	L3	2483
	4/76	S27	37	1	P18	2091
	4/76	S27	18	7	J18	2662
	4/76	S27	18	7	A15	3767
	5/77	S27	19	1	L3	3961
	5/77	S27	19	7	Q1	3995
	6/78	S27	17	7	A15	288
	6/78	S27	17	7	A15	2243
	6/78	S27	17	1	A19	3707
	7/79	S27	17	6	A15	3976
	7/79	S27	17	7	J18	4012
McFarland, D.J.	2/74	07	8	7	P7	3424
	3/75	07	37	1	A7	1841
	3/75	010	37	1	R8	4159
	4/76	012	38	1	A12	4490
	5/77	012	11	1	B18	1043
	6/78	012	27	1	N2	82
	6/78	012	33	7	B6	3356
	6/78	012	35	7	P3	3461

	7/79	012	37	6	A12	3008
	7/79	012	37	1	B18	1820
Marsden, C.D.	3/75	L51	35	7	B21	3367
	5/77	L51	35	7	B21	348
	5/77	L23	35	7	P4	1499
	5/77	L51	35	7	P4	1565
	5/77	L51	33	7	B21	2670
	6/78	L51	35	7	N4	164
	6/78	L51	35	7	N4	979
	6/78	L51	35	7	J32	2027
	6/78	L51	35	7	J32	2090
	7/79	L51	35	7	B28	1320
	7/79	L30	31	8	B18	2051
Morgan, M.J.	2/74	C8	13	7	A12	384
	2/74	C8	17	1	A12	3158
	3/75	C8	13	7	B21	2319
	3/75	C8	17	7	J36	2420
	3/75	C8	8	7	L3	2618
	4/76	C8	13	7	P7	2566
	4/76	C8	13	7	A12	3676
	4/76	C8	13	7	Q1	1492
	4/76	C8	35	7	P4	2494
	4/76	C8	15	7	L3	3686
	4/76	C8	19	6	P2	3823
	5/77	C8	13	7	P7	479
	5/77	C8	15	7	Q1	1637
	5/77	C8	13	7	P7	2792
	5/77	C8	38	1	Q1	3269
	6/78	C8	13	7	D2	1057
	6/78	C8	13	7	Q1	2222
	6/78	D6	13	7	D2	3668
	7/79	D6	13	7	B6	360
Naylor, R.J.	2/74	B29	35	7	N4	266
	2/74	B29	35	7	E7	1209
	3/75	B29	35	7	E7	2218
	3/75	B29	35	7	E7	3368
	4/76	B29	35	7	E7	267
	4/76	B29	35	7	E7	3597
	5/77	B29	33	7	B21	2670
	6/78	B29	35	7	J32	167
	6/78	B29	35	7	E7	2008
	6/78	B29	35	7	E7	3482
	7/79	B29	35	1	J25	249
Nowell, N.W.	2/74	H10	30	7	B6	225
	2/74	H10	1	7	P7	1621
	2/74	H10	1	7	A12	1622
	2/74	H10	2	7	A15	1643
	2/74	H10	1	7	A12	2400
	2/74	H10	1	7	P7	3507
	3/75	H10	36	7	P7	419

	3/75	H10	13	7	B6	468
	3/75	H10	1	7	A15	749
	3/75	H10	25	7	B6	1954
	4/76	H10	36	7	J14	2543
	5/77	H10	25	7	C3	59
	5/77	H10	1	7	B6	4163
	6/78	H10	1	7	B6	422
	7/79	H10	36	7	J14	1331
Oakley, D.A.	3/75	L67	19	7	P7	604
	3/75	L63	18	7	J11	2450
	3/75	L67	13	7	J11	3485
	4/76	L67	33	7	P7	1376
	5/77	L67	33	7	P7	2662
	5/77	L67	13	7	B6	2808
	6/78	L19	33	7	P7	134
	6/78	L19	33	7	P7	3316
	7/79	L63	33	7	P7	3529
	7/79	L63	33	7	P6	3530
	7/79	L67	33	7	E11	3531
Payne, A.P.	2/74	B19	2	7	P7	711
	2/74	G2	36	7	J14	1277
	3/75	G2	36	7	P7	418
	3/75	G2	2	7	A12	1658
	4/76	G2	36	7	J14	3641
	5/77	G2	36	7	J34	404
	5/77	G2	1	7	J14	4173
	6/78	G2	36	7	J14	217
	7/79	G2	36	7	A12	3797
Plotkin, H.C.	2/74	L67	18	7	P7	522
	3/75	L63	18	7	J11	2450
	3/75	L67	13	7	J11	3485
	3/75	L18	15	7	D2	3507
	5/77	L67	13	7	B6	2808
	5/77	L45	33	7	B6	3604
Poole, T.B.	2/74	A11	2	7	A12	710
	2/74	A11	38	7	M6	1890
	2/74	A11	5	7	J38	3590
	3/75	A11	2	7	J38	778
	3/77	A11	24	7	A12	1106
	3/75	A11	13	7	J38	2338
	3/75	A11	2	7	A12	2730
	4/76	A11	8	7	J38	3948
	4/76	A11	2	7	A12	4092
	4/76	A11	12	8	A12	4274
	5/77	A11	40	7	J38	1145
	6/78	A11	7	7	A12	2730
	6/78	A11	1	8	J38	4133
Ridley, R.M.	3/75	L51	19	8	N8	614
	3/75	L51	19	8	N8	2516

	4/76	L51	19	8	B21	3848
	5/77	L51	31	8	E10	3534
	6/78	H4	35	8	B28	3542
	6/78	L51	19	8	E10	3836
	7/79	L51	33	8	N8	222
	7/79	H4	24	8	B28	1082
	7/79	L51	31	8	B18	2053
	7/79	H4	35	8	P22	3759
Robbins, T.W.	2/74	C8	35	7	N3	2141
	3/75	C8	13	7	B21	2319
	3/75	C8	35	7	N7	3404
	5/77	S5	38	7	A15	3293
	5/77	C8	35	7	N2	1546
	5/77	C8	19	7	P22	2904
	5/77	C8	13	7	P7	2790
	5/77	C8	35	7	P4	3672
	6/78	C8	13	7	A15	252
	6/78	C8	35	7	N7	971
	6/78	C8	35	7	P4	3458
	7/79	C8	17	7	P22	1383
	7/79	C8	33	7	J11	3533
Rolls, B.J.	2/74	07	33	7	J11	159
	2/74	07	33	7	J11	161
	2/74	07	8	7	P7	3424
	3/75	07	35	7	P21	354
	4/76	07	27	7	P7	158
	5/77	07	27	7	P4	3494
	6/78	07	27	7	A9	762
	6/78	07	27	7	A9	763
	6/78	07	27	7	P7	3194
Rolls, E.T.	2/74	07	33	7	J11	159
	2/74	07	33	7	J11	161
	2/74	07	31	7	B21	1126
	2/74	07	26	7	P7	2866
	2/74	07	26	7	E11	2870
	2/74	07	26	7	E10	2889
	3/75	07	35	7	P21	354
	3/75	07	26	7	P4	2127
	4/76	07	26	7	N11	2364
	4/76	07	31	8	B21	3443
	4/76	07	26	7	P4	3453
	4/76	07	26	8	P4	3468
	5/77	07	31	8	L4	192
	5/77	07	31	8	E11	195
	5/77	07	26	1	B18	2586
	5/77	07	26	7	B22	2604
	5/77	07	26	8	B18	2651
	6/78	07	31	8	B21	1877
	6/78	07	31	8	B21	3271
	7/79	07	31	8	B21	3446

Roper, T.J.	2/74	C8	17	7	A12	1397
	3/75	C8	5	7	B9	2794
	4/76	C8	17	7	L3	1553
	5/77	C8	5	7	B9	890
	5/77	C8	28	7	P7	1299
	5/77	C8	17	7	J36	3886
	5/77	C8	12	7	B9	440
	6/78	C8	28	7	J38	743
	7/79	S29	8	7	A12	2523
	7/79	S29	17	7	J36	2316
	7/79	S29	8	1	A12	2453
	7/79	S29	17	1	A7	3970
Russell, I.S.	2/74	L67	18	7	P7	522
	3/75	L67	19	7	P7	604
	3/75	L67	38	7	P7	1050
	4/76	L67	33	7	P7	1376
	5/77	L67	33	7	P7	2662
	6/78	L19	33	7	P7	134
	6/78	L19	33	7	P7	3316
	7/79	L67	33	7	P7	3501
	7/79	L63	33	7	P7	3529
Sahgal, A.	4/76	C8	24	6	P21	1170
	4/76	C8	24	8	J36	1185
	4/76	C8	19	8	N2	1646
	5/77	C8	35	6	P21	3645
	6/78	C8	33	8	B21	3367
	7/79	C8	33	8	N8	220
	7/79	C8	35	6	P22	2122
	7/79	C8	19	8	B18	2441
	7/79	C8	20	6	P22	4139
Sanger, D.J.	2/74	L56	35	7	P21	2974
	3/75	B24	17	7	P21	531
	4/76	B24	17	7	Q1	439
	4/76	B24	35	7	J31	1410
	4/76	B24	17	7	J31	1556
	4/76	B24	17	7	P21	2607
	4/76	B24	17	7	P16	3718
	5/77	B24	17	7	B6	523
	5/77	B24	18	7	P22	552
	5/77	B24	17	7	P4	1679
	5/77	B24	8	7	P22	1925
	5/77	B24	18	7	J36	2889
	6/78	C19	17	7	P4	287
	6/78	C19	35	7	P22	2028
	7/79	C19	35	7	P22	258
	7/79	C19	35	7	P4	289
	7/79	C19	35	7	P22	1285
	7/79	C19	38	7	P17	3058
Shillito, E.E.	2/74	C1	25	7	A12	1949
	3/75	C1	35	7	B28	3399

	4/76	C1	6	7	A20	873
	4/76	C1	24	7	A20	1174
	5/77	C1	24	7	A20	3371
	5/77	C1	25	7	A20	3419
	6/78	C1	6	7	A20	2688
	6/78	C1	6	7	A20	2689
	6/78	C1	35	7	N9	3478
	6/78	C1	6	7	A20	4345
	7/79	C1	6	1	Z2	780
Slater, P.J.B.	2/74	S28	8	6	A12	3408
	3/75	S28	8	6	R2	662
	3/75	S29	8	6	B17	2601
	6/78	S28	28	6	A12	63
	7/79	S28	1	7	N2	1571
	7/79	S29	36	1	S4	2199
Smart, J.L.	2/74	M5	6	7	A12	769
	2/74	M5	30	7	N2	2945
	2/74	M5	13	1	B30	3097
	3/75	M5	13	7	B27	1370
	3/75	K2	13	7	B21	1373
	3/75	M5	38	7	L1	1873
	3/75	M5	13	7	D2	3455
	4/76	M5	13	7	P7	385
	4/76	M5	10	7	B6	1076
	5/77	M5	6	7	P7	916
	5/77	M5	13	7	A15	2802
	6/78	M5	13	7	D2	1043
	6/78	M5	13	7	A5	1046
	6/78	M5	13	7	A8	2202
	6/78	M5	13	1	B18	3608
	7/79	M5	13	7	P7	364
	7/79	M5	30	7	P4	2110
	7/79	M5	13	7	B27	2258
Steel, E.	2/74	C16	36	6	J14	1275
	3/75	C16	24	6	J14	3052
	5/77	C16	36	6	H3	1576
	5/77	C16	5	6	J34	4282
	5/77	C16	5	6	J34	4283
	7/79	C16	5	6	A7	4633
Stolerman, I.P.	2/74	B24	35	7	P21	302
	4/76	B24	35	7	B28	2500
	4/76	B24	18	7	P4	3771
	5/77	B26	35	7	B28	3722
	6/78	B26	35	7	B21	2095
	6/78	B26	18	7	P4	2280
	6/78	B24	18	7	B28	2289
	6/78	B26	18	7	P4	3767
	7/79	B26	18	7	P4	431
	7/79	B26	18	7	P4	2357

Swanson, H.H.	2/74	G2	36	7	J14	1277
	3/75	B19	6	7	A12	860
	3/75	B19	13	7	D2	3465
	4/76	B19	9	7	Z1	1048
	6/78	B19	36	7	J14	2135
	6/78	B19	7	7	A8	4397
	7/79	B19	36	7	B12	320
	7/79	B19	13	7	J14	3896
Thorpe, W.H.	2/74	C12	1	6	S2	675
	2/74	C12	37	1	N12	3758
	5/77	C12	37	6	B18	1074
Weiskrantz, L.	3/75	06	37	1	P6	994
	3/75	07	38	8	Q1	1882
	3/75	07	24	7	B21	1916
	3/75	07	17	7	Q1	2404
	3/75	07	19	8	N8	2517
	4/76	07	19	8	N8	555
	4/76	07	28	7	B15	2281
	4/76	07	33	7	B15	3499
	6/78	07	33	7	B19	3370
Williams, D.I.	2/74	H9	13	7	D2	1334
	3/75	H9	6	7	A12	870
	3/75	H9	13	7	B6	3456
	3/75	H9	13	7	D2	3475
	5/77	H9	6	7	P20	2147
	6/78	H9	6	7	B9	2685
Wood-Gush, D.G.M.	2/74	E3	7	6	A12	3650
	3/75	E3	35	6	A20	3326
	3/75	E3	10	6	A12	4132
	3/75	E3	10	6	A12	4133
	4/76	E3	5	6	A20	826
	4/76	E3	10	6	V2	2052
	4/76	E3	10	6	A12	4411
	5/77	E3	12	6	A20	2207
	6/78	E3	5	6	A20	2646
	6/78	E3	8	6	A20	2437
	6/78	E3	2	6	A12	1356
	7/79	E3	7	6	B16	810
	7/79	E3	40	6	B16	1034
	7/79	E3	33	6	B12	1245
	7/79	E3	33	6	A12	2084

APPENDIX VI

Individual papers on animal behaviour recorded in Animal Behaviour Abstracts, Volume 8 (1980), with details of:
a. Author's name b. Work base c. Field of interest
d. Animals used e. Journal in which paper published, and
f. Abstract reference number.

Notes:
i) Keys to the four coded categories (b-e) are supplied below (pp. 318-344).
ii) Names of sole authors are asterisked. The linking of partners in authorship can be made via the abstract reference number.
iii) Some authors were foreign visitors, but all work recorded here was carried out in the U.K. or its waters.
iv) Changes of name through marriage have not been identified or indicated.
v) Columns g. to m. show consecutively the number of abstracts made of each author's work in the previous years' editions of Animal Behaviour Abstracts, Volumes 2 (1974) to 7 (1979). Details for authors whose work was also abstracted in Behavioural Biology Abstracts (Volume 1) appear in Appendix IV.
vi) Column n. shows the total number of abstracts made of each author's work between the sample years 1973 and 1980 (inclusive), also taking into account information from Appendix IV.

a	b	c	d	e	f	g	h	j	k	l	m	n
Abramson, M.*	P9	3	6	I1	87							1
Adams, C.E.	C1	13	7	L1	479							3
Agius, L.*	018	9	2	M5	1515							1
Aitken, L.M.	L17	25	6	J13	5171	1		1				3
Al-Maliki, S.	S31	2	7	P4	69						1	3
Al-Maliki, S.	S31	2	7	A12	71							
Albon, S.D.	C14	2	7	B9	1290						1	3
Albon, S.D.	C14	5	7	N2	4267							
Anderson, D.M.	C16	5	8	L1	188							1
Anderson, J.R.	S20	7	8	S3	2708		2	1	1		2	7
Andrew, R.J.	S28	36	7	A12	1049							16
Andrew, R.J.	S28	36	6	B9	5563							
Annable, A.	M8	17	7	J36	3158							1
Archer, J.*	P8	10	7	B29	1620							21
Archer, J.*	P8	40	1	B18	2348							
Archer, M.E.*	P9	7	3	E5	4316							3
Armitage, J.P.	L62	21	2	F1	659				1	1		3
Arnold, G.P.	L75	21	5	J1	1904		2			1	3	7
Ashe,J.*	P9	1	4	A23	23			3			1	5

Atkinson, R.J.A.	M13	28	5	B18	3432							6
Atkinson, W.D.	E8	9	3	H2	4611							1
Avery, R.A.*	B31	9	4	S4	363					1		2
Avrith, D.B.	C10	35	7	N2	5461				1		2	4
Aylesbury, L.J.	O19	38	1	B3	1094							1
Bagley, L.	P1	39	7	G4	1157							1
Baker, H.F.	H4	35	8	B15	2196							3
Baker, H.F.	H4	35	8	P22	3708							
Baker, H.F.	H4	19	8	P22	5010							
Baker, P.S.*	L14	22	3	J13	701							3
Baker, P.S.*	L14	22	3	J13	702							
Baker, P.S.*	L14	22	3	J13	705							
Baker, R.R.	M9	21	3	A12	670						1	3
Baker, R.R.	M9	11	6	R8	1657							
Baker, R.	S14	1	3	J9	3963			2		1	6	10
Baldwin, B.A.	C1	4	7	A12	100							26
Baldwin, B.A.	C1	34	7	P7	930							
Baldwin, B.A.*	C1	19	7	P7	3211							
Baldwin, B.A.*	C1	39	7	J4	3869							
Baldwin, B.A.	C1	33	7	J34	5406							
Balfour,E.	S6	5	6	O5	1357							1
Bannister, L.H.	O3	21	2	A4	3249							1
Barnard, C.J.*	N14	11	6	A10	1655						1	5
Barnard, C.J.*	N14	8	6	B25	2807							
Barnard, C.J.*	N14	8	6	A12	2818							
Barnard, C.J.	N14	37	1	J37	3759							
Barrass, R.*	S24	11	3	B18	1651			2	2			5
Bateson, P.P.G.*	C12	13	6	A15	476							26
Bateson, P.P.G.*	C12	13	1	A12	1691							
Bateson, P.P.G.	C12	13	7	B5	3087							
Bateson, P.P.G.	C1	34	6	P7	3598							
Beeston, D.C.	B25	28	2	A12	778							2
Beeston, D.C.	B25	28	2	A12	779							
Bell, F.R.	L55	33	7	P7	5410	1					1	3
Bell, R.	B15	2	7	P12	4062				1		1	3
Bennet-Clark, H.	O10	1	3	A12	2395	1		2	1	1		6
Bennett, D.B.	B40	9	2	J28	2859							1
Bennett, R.C.	O7	38	7	P7	5711							1
Benton, D.	S30	4	7	B12	1324				1	1	4	8
Benton, D.	S31	36	7	J14	2220							
Bernays,E.A.*	L14	38	3	E2	5685							8
Berryman, J.C.	L5	13	6	Q1	4815							9
Bertram, B.C.R.*	C14	5	6	N2	158			1	2		1	6
Bertram, B.C.R.*	C14	7	1	B18	1399							
Best, S.M.	S28	36	7	A12	1049							1
Bevans, E.	S4	8	3	O1	2740							1
Bibby, C.F.*	S6	9	6	B25	1562							1
Bibby, C.J.	S6	8	6	J3	4498				1			2
Binns, E.S.*	L7	9	2	A1	2873					3		5
Binns, E.S.*	L7	21	3	E5	5055							
Birke, L.I.A.*	S28	36	7	A12	1048	1	1				1	5
Birke, L.I.A	S28	36	7	A12	1049							
Birkhead, T.R.*	S11	5	6	A12	168		2	1	1	3	1	9
Bishop, J.A.	L9	9	7	L5	4699							1

Black, A.J.	E3	25	6	B5	3362	1	2			2		6
Blaxter, J.H.S.	O1	13	5	B18	3063							4
Blight, M.M.	S26	1	3	E3	14						1	2
Blizard, R.A.	B9	1	7	J9	2452							1
Blundell, J.E.	L4	35	7	P4	3706							9
Blundell, J.E.	L4	8	7	B28	4504							
Blundell, J.E.	L4	35	1	B18	5474							
Boakes, R.A.	S27	17	7	R4	560							12
Boakes, R.A.*	S25	17	1	B18	3125							
Boakes, R.A.	B10	17	7	P16	4924							
Booth, D.A.*	B18	37	1	B18	3758							33
Booth, D.A.*	B24	27	1	B18	5192							
Booth, J.E.	L15	30	7	P7	3480				1	1		3
Booth, W.D.	C1	33	7	J34	5406							1
Bourne, W.R.P.	A7	21	6	R7	5074			1			1	3
Bowden, J.*	H2	28	3	B34	782						1	2
Bowles, M	M14	8	6	A12	1478							1
Bowmaker, J.K.*	L53	24	6	B18	5130							1
Brace, R.C.	N14	4	2	A12	94						1	2
Bradbury, K.	P9	5	3	E5	1342							1
Bradley, P.	C1	30	6	B21	2043							1
Brady, J.N.	L46	28	3	P5	5229	2	3					7
Brain, M.V.*	N11	7	3	B18	1408	1						2
Brain, P.F.	S31	2	7	P4	69							30
Brain, P.F.	S31	2	7	A12	71							
Brain, P.F.	S31	2	7	B9	1289							
Brain, P.F.	S30	4	7	B12	1324							
Brain, P.F.	S31	36	7	J14	2213							
Brain, P.F.	S31	36	7	J14	2220							
Brain, P.F.	S31	36	7	P7	3744							
Brain, P.F.	S31	1	7	J14	4019							
Brain, P.F.*	S31	36	1	B18	5558							
Brain, P.F.*	S31	36	1	B18	5559							
Branford, J.R.	I1	28	2	B18	3399							1
Brener, J.	H9	18	7	P23	4950							1
Brennan, A.	N3	40	3	H4	5781							1
Brimblecombe, R.	P7	19	7	G2	5020							1
Bristowe, W.S.*	N11	3	3	P10	79							1
Broadhurst, P.L.	B24	18	7	B10	599			2	1		2	7
Broadhurst, P.L.	B24	35	7	J35	2162							
Broady, P.A.	N11	8	3	B23	2747							1
Brockman, H.J.	O12	11	3	J37	1639	1			1		1	4
Broom, D.M.*	R4	38	1	B16	1106		1		2	3	1	11
Broom, D.M.	R4	9	5	A12	2935							
Broom, D.M.*	R4	28	6	A12	3446							
Broom, D.M.	R4	25	7	J28	5177							
Brown, C.A.J.	L30	8	7	J7	2823							1
Brown, K.*	B11	1	1	B18	3947							5
Brown, K	B15	2	7	B15	4062							
Brown, M.W.	C1	32	6	B21	2084						1	2
Brown, R.M.	C8	35	7	B21	3633			1				2
Brownstein, M.J.	C8	35	7	B21	3633							1
Bruno, D.W.	L28	5	3	J23	4164							1
Bryant, M.J.	R2	39	7	A20	3859							5

Burk, T.	N14	37	1	J37	3759	1		1				3
Burley, R.A.*	C16	5	7	B9	4275							1
Burnet, B.	S9	5	3	E9	135							11
Byrne, E.A.	M5	13	7	P7	4868						1	2
Cadbury, C.J.	S6	5	6	O5	1357			1		1		3
Caincross, K.D.	M16	35	7	P4	1010		4	1		2		8
Caro, T.M.	C12	38	1	B9	2288				1			3
Caro, T.M.*	C12	13	7	Z1	4847							
Carr, A.T.*	L5	8	7	B18	2349							1
Carrera, J	L30	8	7	J7	2823							1
Carter, C.J.	B33	33	7	N4	2114						1	2
Cartwright, B.A.	S29	24	3	J16	5112							1
Castle, M.E.	N11	39	7	G4	3873							1
Catchpole, C.K.*	L41	1	6	S4	4008	2	1		2		1	7
Chalkly-Maber, C.	A3	25	7	A15	1974							1
Chamove, A.S.	S20	7	8	S3	2708							13
Chandler, R.F.*	P9	40	6	B25	2358							1
Chapman, C.J.	A2	22	2	P13	695							6
Charlesworth, B.*	S29	11	1	A10	1628						2	3
Charlwood,J.D.	S29	5	3	P5	117							1
Cherrett, J.M.	B3	2	3	A12	1279	1	1				1	4
Clancy, A.	B7	18	7	J32	577				1			2
Clapham, C.*	L2	21	6	R5	3267							1
Clark, C.R.	H10	36	7	J14	2215			1			1	3
Clark, F.	L6	5	6	I1	4212							1
Clayton, D.A.	S28	36	6	B9	5563			1	2		2	6
Clements, A.	D5	24	7	A12	732							1
Clifton, P.G.*	S29	8	6	A12	301							4
Clifton, P.G.*	S29	8	6	A12	302							
Clifton, P.G.*	S29	8'	6	A12	308							
Clifton, P.G.*	S28	8	6	A12	2800							
Clingbine, G.	L32	35	5	P7	3625				1			2
Cloudsley-Thompson, J.L.*	L41	28	4	J8	2009				1	1	2	5
Clutton-Brock, T.	C14	2	7	B9	1290	1	3	2	2		3	14
Clutton-Brock, T.	C14	5	7	N2	4267							
Clutton-Brock, T	C14	30	8	J38	5313							
Coaker, T.H.	P4	25	3	E2	744							3
Coaker, T.H.	P4	25	3	E2	747							
Cockerill,R.A.	C14	6	7	A12	194							1
Cole, L.R.*	P9	9	3	E5	1543							1
Coleman, A.E.	P9	5	6	W1	2611							1
Coles, R.B.	L17	25	6	J13	5171	2						3
Coles, R.	L17	25	6	T2	5172							1
Collett, T.S.	S29	24	4	J13	729	1		2	1			7
Collett, T.S.	S29	24	3	J16	5112							
Collett, T.S.	S29	24	4	R9	5123							
Collins, G.G.S.	L56	35	7	B28	5472							1
Collis, K.A.*	N1	39	7	A20	3872			1			1	3
Colwill, R.M.	C8	18	7	Q1	4956						1	2
Conn, D.L.T.*	O11	5	3	E5	113							1
Connally, S.	H9	18	7	P23	4950							1
Cook, A.*	B10	21	2	M1	1893		1	1		1	1	5
Cooper, S.J.	B24	35	7	P22	978	4		1	1		3	17

Cooper, S.J.	B24	35	7	P22	1016							
Cooper, S.J.	B24	35	6	P22	2156							
Cooper, S.J.	B24	35	7	P22	2172							
Cooper, S.J.	B24	35	7	J32	3665							
Cooper, S.J.	S27	35	7	P22	3666							
Cooper, S.J.	B24	8	7	P4	4537							
Cooper, S.J.*	B11	35	1	B18	5476							
Cooper-Driver, G.	L14	8	3	B14	2765							1
Cooter, R.J.*	L14	22	3	J13	703	1						2
Corfield-Sumner,P.	C19	27	7	P4	767				2		3	6
Coulson, J.C.	D7	7	6	S6	2685					1		2
Cowan, P.J.	A9	39	6	A14	5728	5	1			2	1	10
Cox, B.	M6	34	7	N7	957	1		2		2		7
Cox, B.	M6	35	1	P4	1010							
Cram, A.	N11	9	2	M3	4577				1			2
Cresswell, W.	P9	5	3	E5	1342							1
Crisp, D.J.*	A13	3	2	S6	2496	1						2
Crow, T.J.	L56	33	7	B21	906	2	1	2	2	2	1	11
Crowden, A.E.	R4	9	5	A12	2935							1
Crump, A.J.	L46	28	3	P5	5229			1				2
Curds, C.R.*	L12	3	2	S6	2497					1		2
Cutler, M.G.	G1	35	7	P22	3675			5	1	1	2	11
Cutler, M.G.	G1	35	7	P22	3676							
Dank, G.R.	C12	38	1	B9	2288							1
David, C.T.*	L46	22	3	P5	3299							1
Davies, L.	D7	28	3	J28	5226							1
Davies, N.B.*	O13	3	1	B18	1295			2	2	3	2	11
Davies, N.B.	C1	5	4	A12	2581							
Dawkins, R.	O12	1	1	B18	1204							8
Dawkins, R.	O12	11	3	J37	1639							
Dawkins, R.*	O12	37	1	Z1	5626							
Deacon, R.M.J.	B28	35	7	P22	2189							1
Deag, J.M.*	N11	9	8	B18	2983				1			2
Deakin, J.F.W.	L31	30	7	P4	829						1	3
Deakin, J.F.W.	L56	33	7	B21	906							
Dean, J.*	A7	38	1	P7	3796							4
Dean, J.*	A7	2	3	J9	4045							
Dean, J.*	A7	8	4	J13	4455							
Dean, J.*	A7	8	4	J13	4456							
Dean, P.*	S10	33	8	E10	890		2		1		2	7
Dean, P.	S10	33	7	B5	5374							
Dearing, M.F.	C8	18	7	A15	1820		1					2
Dennis, B.	L55	33	7	P7	5410							1
Dennison, S.F.*	P9	38	1	P1	5663							1
De Wit, H.	O7	35	7	Q1	974			1		1		3
Dickinson, A.	C8	18	7	A15	1820							19
Dickinson, A.*	C3	17	1	B18	3124							
Dickinson, A.	S25	17	1	B18	3133							
Dickinson, A.	C8	18	7	Q1	4956							
Dimond, S.J.*	C19	11	1	N12	1635							4
Dimond, S.J.*	C19	30	1	B18	3472							
Dixon, A.F.*	L73	36	8	A8	3749							5
Dixon, F.	D7	7	6	S6	2685							1
Dobbing, J.*	M4	13	1	B18	1696	1	3	1		2	1	9

Dorsett, D.A.*	A13	28	2	B18	3403	3	2	2	1			9
Douglas, J.M.	L35	38	1	A12	2271						1	2
Drewek, K.J.	B24	35	7	J35	2162							1
Drewett, R.F.	D6	5	7	P7	2627							12
Dunstone, N.	D5	24	7	A12	732		1	1		2	1	7
Dunstone, N.	D5	8	7	A12	2826							
Eastwood, L.	S9	5	3	E9	135	1			2	1		5
Eberhart, J.A.	C6	36	8	J14	5597							1
Einon, D.F.	D6	33	7	Q1	5390			3	3	3	1	11
Elgar, R.J.*	P9	5	6	A25	2604			1				2
Elkins, N.*	L74	21	6	B25	3268			1	1			3
Elwood, R.W.*	B12	6	7	D2	196			1	1	2		7
Elwood, R.W.*	R4	6	7	B5	1385							
Elwood, R.W.	B12	9	2	A12	1511							
Erichsen, J.T.	O12	8	6	J3	4483				1			2
Esslemont, R.J.	R2	39	7	A20	3859							1
Ettlinger, G.	L51	19	8	N8	3224							23
Evans, M.C.W.	L62	21	2	F1	659							1
Evans, M.E.*	S12	5	6	W1	2612			2			1	4
Evans, P.R.	D7	21	6	B17	1917	1				1		4
Evans, P.R.*	D7	8	6	B18	2806							
Evans, S.M.	N6	7	6	A12	4333							7
Evans, S.M.	N11	9	2	M3	4577							
Ewart, F.G.	G1	35	7	P22	3675						2	4
Ewart, F.G.	G1	35	7	P22	3676							
Eysenck, H.J.*	L51	37	1	B4	2245							3
Feare, C.J.	W4	8	6	O5	1472					1	1	3
Fedak, M.A.	C2	22	1	N2	3294							1
Feldon, J.	O7	35	7	Q1	974							4
Feldon, J.	O7	33	7	Q1	3580							
Feldon, J.	O7	33	7	Q1	3581							
Feldon, J.	O7	33	7	E10	5389							
Ferguson, A.W.	H2	1	3	J5	2401							2
Ferguson, A.W.	H2	1	3	P5	2408							
File, S.E.	L31	30	7	P4	829							36
File, S.E.	L56	33	7	B21	906							
File, S.E.	L31	33	7	B5	3567							
File, S.E.	L56	35	7	P4	3631							
File, S.E.	B28	35	7	P4	3632							
File, S.E.*	L56	36	7	B21	3729							
File, S.E.	L56	18	7	P7	4979							
File, S.E.	L56	35	7	B28	5472							
Fish, J.D.*	A11	28	2	J27	3410		1		1			3
Fitzsimons, J.T.	C10	35	7	N2	5461			1		5	2	9
Forster, C	M6	35	7	P4	1010					1		2
Forsythe, T.G.*	M9	1	3	E5	2393					1		3
Forsythe, T.G.*	P9	1	3	C5	2394							
Fox, J.E.*	B22	25	7	P7	3363							2
Francis, R.L.	B24	35	7	P22	978		1	1	1		1	9
Francis, R.L.	B24	35	7	P22	2172							
Francis, R.L.	B24	35	7	J32	3665							
Francis, R.L.	S27	35	7	P22	3666							
Francis, R.L.*	B11	38	7	P7	3830							
Franklin, R.V.	B24	18	7	B10	599							1

Free, J.B.	H2	1	3	J5	2401							13
Free, J.B.	H2	1	3	P5	2408							
Freeman, R.D.	C10	24	7	E10	5140							1
Gaffan, D.*	07	20	8	L3	3246							8
Garson, P.J.	N7	9	6	I1	4665						1	2
Gates, S.*	E12	9	7	M2	405							1
Gentle, M.J.	E3	25	6	C3	1956	1	1	2	1		3	11
Gentle, M.J.*	E3	25	6	C3	1957							
Gentle, M.J.*	E3	39	6	B31	5733							
Gibbs, M.E.	M15	30	6	N9	5287	1		3	5	4	1	15
Gibson, R.N.	01	13	5	B18	3063	1			2			5
Gibson, R.N.*	01	28	5	B18	3440							
Girling, D.J.*	S13	5	3	E5	124							1
Gittins, S.P.	C21	5	4	J3	4200							1
Glen, D.M.	B38	8	6	J7	304			1				2
Glencross, R.G.	R2	39	7	A20	3859							1
Goldberg, D.M.	B26	35	7	N7	5504					1		2
Goldberg, S.R.	B26	35	7	N7	5504	1	1	2	3	3		11
Goodale, M.A.	S2	33	7	J11	5375		1			2	2	6
Goudie, A.J.	L8	30	7	P22	832	3	2	4		1	2	15
Goudie, A.J.*	L8	18	1	N7	3164							
Goudie, A.J.*	L8	18	7	I4	3191							
Graeff, F.G.	07	18	6	P22	572		2	1	1		3	8
Grafen, A.*	020	37	1	A12	1072						1	3
Grafen, A.	012	11	3	J37	1639							
Grant, S.A.	P1	39	7	G4	1157							1
Gray, J.A.	07	35	7	Q1	974							16
Gray, J.A.*	07	10	7	B29	1613							
Gray, J.A.*	07	40	7	B29	2341							
Gray, J.A.*	07	40	1	B29	2342							
Gray, J.A.*	06	32	1	B18	3500							
Gray, J.A.	07	33	7	Q1	3580							
Gray, J.A.	07	33	7	Q1	3581							
Gray, J.A.	07	33	7	E10	5389							
Green, A.R.	W2	35	7	N7	2168		2	4	2	2	3	14
Green, R.E.	S6	8	6	J3	4498			1	1			3
Greenway, A.R.	H2	25	3	E2	745	1		2			1	5
Greenwood, J.J.D.	D2	8	6	J3	299				1			3
Greenwood, J.J.D.	D7	5	6	L5	2603							
Greenwood, P.J.	013	11	6	A12	442				2		4	9
Greenwood, P.J.	013	5	6	04	1355							
Greenwood, P.J.	S29	11	1	B18	1629							
Greer Walker, M.	L75	21	5	J1	1904						1	2
Greig-Smith, P.W.*	S29	7	6	I1	1413						6	8
Greig-Smith, P.W.*	S29	40	6	I1	5788							
Griffiths, C.	L38	13	7	B21	507							1
Griffiths, D.C.	H2	25	3	E2	745						1	2
Groot, S.J.de	01	13	5	B18	3063			1				2
Gubbins, S.J.	S29	28	3	P5	5225		1			1		3
Guillamon, A.	07	35	7	Q1	974	1						2
Guinness, F.E.	C14	6	7	A12	194			1			1	4
Gurnell, J.*	L69	12	7	F3	461		1				1	4
Gurnell, J.*	L69	38	7	J38	1136							
Gurney, W.S.C.*	S22	37	1	T1	2240							1

Hall, G.*	Y3	19	7	A12	617	3	3	2	1	1	3	15
Hall, G.	C8	17	7	A15	4916							
Hall, M.J.	C14	6	7	A12	194							1
Hall, M.J.R.*	P9	32	3	P5	5328			1				2
Halliday, T.R.*	M14	5	1	B18	1329	1	1	1	3	1	2	11
Halliday, T.R.	C1	5	4	A12	2581							
Halliwell, M.	B33	38	7	P7	5710							1
Hambley, J.	M15	30	6	N9	5287		1		1			3
Hamid, R.B.	L70	39	6	B31	5734							1
Handley, S.L.	A15	35	7	P22	2165						2	3
Harden Jones, F.	L75	21	5	J1	1904					1	1	3
Hardman, B.	D2	8	6	J3	299							1
Harris, M.P.	A7	21	6	R7	5074							4
Harris, P.R.*	P9	8	6	B17	4469							1
Harrison, J.D.	T2	21	6	B17	680							2
Harrison, J.D.	T2	21	6	B17	681							
Harrison-Read, P.*	L36	32	7	B21	871							1
Hart, T.	C8	35	7	B21	3633						1	2
Hartley, D.J.	L9	9	7	L5	4699							1
Harvey, P.H.	013	11	6	A12	442		3	1	2		5	16
Harvey, P.H.	013	5	6	04	1355							
Harvey, P.H.	S29	11	1	B18	1629							
Harvey, P.H.	C14	5	7	N2	4267							
Harvey, P.H.	C14	30	8	J38	5313							
Harzem, P.	B4	17	1	J36	1750		2	3	1	2	2	11
Hassell, M.P.	L49	8	3	A18	1444							3
Haug, M.	S31	36	7	J14	2213						4	7
Haug, M.	S31	36	7	P7	3744							
Haug, M.	S31	1	7	J14	4019							
Hauski, I.*	010	9	3	03	4619			1				2
Havukkala, I.*	L46	21	3	A14	5050				2			3
Hawkes, C.	P4	25	3	E2	744							3
Hawkes, C.	P4	25	3	E2	747							
Hawkin, C.	E3	25	6	C3	1956							1
Heading, C.E.	L32	35	5	P7	3625				1			2
Henty, C.J.*	S19	8	6	B17	4492			1	1	1		4
Hepworth, D.	C20	38	3	B3	3813							1
Herberg, L.J.	L30	34	7	E7	942							17
Herbert, J.	C6	28	7	B21	3451							11
Herbert, P.D.N.	P9	9	3	L5	349							1
Hewett, T.D.	L51	19	8	N8	3224							1
Hewson, R.	L30	9	7	J7	4696			1			1	3
Higgins, R.McR.*	L26	1	6	I1	3989							1
Hildrew, A.J.	N10	9	3	J3	2889						1	2
Hinde, R.A.*	C16	13	8	R4	1727							29
Hodgson, J.	P1	39	7	G4	5741							2
Hodgson, J.	P1	39	7	G4	5742							
Holden, M.J.	L75	21	5	J1	1910							1
Holloway, J.D.	P9	9	3	L5	349							1
Holmstroem, W.F.	B25	28	2	B18	3406							1
Hope Jones, P.*	P9	7	6	W1	4327							1
Horn, G.*	C1	13	6	R4	477							15
Horn, G.	C1	30	6	B21	2043							
Horn, G.	C1	32	6	B21	2084							

Horn, G.	C1	34	6	P7	3598							
Horrod, R.G.	L75	21	5	J1	1910							1
Horsely, D.T.	D2	8	6	J3	299							1
House, S.M.	S15	9	4	O2	4630							1
Houston, A.I.	O12	8	6	J3	4483			1	1		1	4
Howard, A.E.	B40	9	2	J28	2859							1
Howard, H.W.*	P9	9	2	C9	4585							1
Howard, R.W.*	N11	40	7	J38	2363				2		2	5
Howe, S.	C16	6	8	B9	4302							1
Howell, P.A.	S31	36	7	J14	2220							1
Howell, T.	A2	22	2	P13	695							1
Howse, P.E.	S14	7	3	I2	209	1	1	6			6	18
Howse, P.E.*	S14	7	3	S6	1406							
Howse, P.E.	S14	8	3	A12	1440							
Howse, P.E.	S14	1	3	J9	3963							
Hudson, P.J.*	O13	6	6	J3	2645							1
Hudson, R.	T2	21	6	R5	5083						2	3
Hughes, R.N.*	B3	37	1	A10	1069	1	1	2	3		2	10
Hunter Jr, M.L.	L34	37	1	A12	3754							2
Hunter Jr, M.L.	N7	9	6	I1	4665							
Huntingford, F.A.*	G4	2	5	A8	64			3	1	1		6
Hyde, J.R.G.	L31	30	7	P4	829					1	1	5
Hyde, J.R.G.	L56	18	7	P7	4979							
Hyde, J.R.G.	L56	35	7	B28	5472							
Ince, S.A.	S28	1	6	B9	2427							1
Inglis, I.R.	W4	8	6	O5	1472		1	1	1	2	1	7
Ironmonger, J.W.	L9	8	2	H4	4388							1
Iversen, S.D.	C8	34	7	N11	965							43
Iversen, S.D.	W2	35	7	N7	2168							
Iversen, S.D.	N2	36	6	C6	3720							
Jaffe, K.	S14	8	3	A12	1440							1
Jamieson, W.S.	P1	39	7	G4	5741							2
Jamieson, W.S.	P1	39	7	G4	5742							
Jawaharlal, K.	P5	35	7	J32	5537							1
Jeffery, G.	S27	17	7	R4	560							1
Jennings, T.	N6	7	6	A12	4333							1
Jervis, M.A.*	C17	5	3	E4	128							1
Johnson, E.	R4	25	7	J28	5177							1
Johnson, F.N.*	L3	35	1	N10	2150							6
Johnson, F.N.*	L3	35	5	I3	2152							
Johnson, F.N.*	L3	35	7	I3	5526							
Jones, M.D.R.	S29	5	3	P5	117	1	3	1		2		9
Jones, M.D.R.	S29	28	3	P5	5225							
Jones, O.T.	S14	9	3	A17	4604							2
Jones, O.T.*	S14	9	3	E1	4605							
Jones, R.B.*	E3	24	6	A12	3332							18
Jones, R.B.	E3	25	6	B5	3362							
Jones, S.E.	S31	36	7	J14	2220							1
Jutsum, A.R.*	B3	2	3	A12	62						1	3
Jutsum, A.R.	B3	2	3	A12	1279							
Kacelnik, A.	L34	37	1	A12	3754						2	3
Katz, H.B.	M5	13	7	D2	505							1
Keighley, P.	L62	21	2	F1	659							1
Kelley, A.E.	C8	34	7	N11	965						2	3

Keverne, E.B.	C6	25	7	J34	1971				3	1	4	10
Keverne, E.B.	C6	36	8	J14	5597							
Key, C.	P9	39	7	A20	3860							1
Kheirallah, A.M.*	M9	9	2	R3	1513							1
King, B.	N12	38	7	P4	1138						1	2
Kirby, R.M.	P4	17	7	P17	4886					1		2
Knowlton,N.	C12	37	1	N2	2239							1
Koob, G.F.	C8	33	7	N2	5393		2	2	4	3	4	16
Krebs, J.	N11	9	6	B18	2942					1		2
Krebs, J.R.	O12	1	1	B18	1204		4	3	4	1	1	17
Krebs, J.R.*	O13	8	1	B18	1433							
Krebs, J.R.	B3	1	6	J2	4012							
Krebs, J.R.	O12	8	6	J3	4483							
Kruk, Z.L.	L27	33	7	P22	2113	1						2
Kruuk, H.	L30	8	7	J7	2823			2		1	3	7
Kumar, R.	L51	35	7	P22	973							5
Kumar, R.	L51	35	7	P22	3690							
Langslow, D.R.*	A1	21	6	B17	3286					1		2
Last, J.M.*	L75	8	5	M5	2788							1
Latham, C.J.	L4	35	7	P4	3706					1	2	6
Latham, C.J.	L4	8	7	B28	4504							
Latham, C.J.	L4	35	1	B18	5474							
Latimer, W.*	A16	1	3	J28	3957					1		2
Laurence, B.R.	L28	5	3	J23	4164							1
Laverack, M.S.	S3	25	2	M3	5152							1
Lawson, H.M.*	D1	8	6	A17	293							1
Lazareno, S.*	R3	35	7	P22	3656							1
Lazarus, J.*	N6	9	6	A12	399							6
Lazarus, J.*	N6	3	6	B9	2510							
Lea, S.E.G.*	E13	8	6	A12	309		1	2	3		1	8
Lee, A.J.	B33	38	7	P7	5710							1
Lee, J.	E4	8	2	P13	240	1		1	1			4
Lee, P.C.	C12	4	8	A12	103						1	2
Lee, T.F.	M6	34	7	N7	957							1
Legg, C.R.*	L19	33	7	B21	3592			1	1	2		5
Leonard, B.E.	L51	13	7	P7	4855			3	3	4	3	14
Leone, C.M.L.	O7	18	6	P22	572							1
Leroy, Y.	O10	1	3	A12	2395		1		2	1	1	6
Leslie, J.C.	B10	17	7	P16	4924							4
Lewis, B.	L17	25	6	T2	5172							1
Lewis, J.W.	L54	38	7	J38	5694							1
Lewis, M.E.	C8	35	7	B21	3633						1	4
Lewis, M.E.	N2	36	6	C6	3720							
Lewis, M.E.	C10	35	7	N2	5461							
Lieberman, D.A.	S19	19	7	J18	1850							1
Linaza, J.	B10	17	7	P16	4924							1
Linkens, D.A.*	S8	38	1	J22	1092							1
Livett, B.H.	P7	19	7	G2	5020							1
Lloyd, S.L.	H2	25	3	E2	745						1	2
Lock, A.	S29	24	4	J13	729							2
Lock, A.	S29	24	4	R9	5123							
Lockie, I.	L30	1	6	I1	39							1
Longden, A.	L56	33	7	B21	906							1
Longhurst, C.	S14	7	3	I2	209					1	3	6

Longhurst, C.	S14	1	3	J9	3963							
Lowe, C.F.	B4	17	1	J36	1750		2	2	1	2	2	10
Lowman, B.G.	E9	39	7	A20	1167							1
Lubbock, R.*	C1	25	2	J16	3343							2
Lubbock, R.*	C1	9	5	R9	4642							
Luff, M.L.*	N4	12	3	A17	4780					1	1	3
Lynch, B.	D2	8	6	J3	299							1
Macdonald, D.W.*	O12	1	7	Z1	2455				2	1	1	6
Macdonald, D.W.*	O10	7	7	N2	4341							
Macdonald, M.A.*	A4	7	6	O5	4328					1		2
Mac Iver, R.M.	P9	39	7	A20	3860							1
Mackintosh, J.H.*	N11	7	7	B18	2689	1	1	5	2	2		13
Mackintosh, J.H.	G1	35	7	P22	3676							
Mackintosh, N.J.	S27	17	7	Q1	563	2	1	3	2	3	3	16
Mackintosh, N.J.	S25	17	1	B18	3133							
Macleod, N.K.	L31	30	7	P4	829							2
Macleod, N.K.	L56	35	7	B28	5472							
Macnair, M.R.	E12	37	1	A12	2243					2		4
Macnair, M.R.	L9	37	1	A12	3762							
Maddison, S.	O7	32	8	B21	2095					1	1	3
Main, J.	A2	22	2	P13	695							1
Makepeace, M.	A4	7	6	A12	212							1
Mann, D.	L5	13	6	Q1	4815							1
Marquiss, M.	A1	5	6	J7	4226				1		1	3
Marsden, C.A.	N12	38	7	P4	1138		1	1		1	2	6
Martin, G.R.	S27	24	6	B18	5131	3	2			1		7
Martin, J.B.	B16	39	7	V2	5738	1	1		1		1	5
Martin, R.D.*	L59	11	8	B18	1662		1					2
Mathers, N.F.	E4	8	2	P13	240		1					2
Matty, A.J.*	A14	30	5	B18	3475							1
Mayes, A.*	M8	40	1	B18	2350							5
Mayes, A.	L5	13	6	Q1	4815							
Maynard Smith, J.*	S29	37	1	R9	3753	1			1		1	4
Mc Cabe, B.J.	C1	34	6	P7	3598						1	2
Mc Carthy, T.K.	N10	2	2	O2	4043							1
Mc Caughey, W.J.	B19	39	7	V2	5738							1
Mc Clean, A.	B12	9	2	A12	1511							1
Mc Cleery, R.H.*	O13	27	1	B18	1978			1		1		3
Mc Clelland, A.	B24	8	7	P4	4537							1
Mc Elhone, M.J.*	B3	8	2	C2	4391							1
Mc Intosh, D.C.	S19	19	7	J18	1850							1
Mc Lachlan, A.J.	N3	40	3	H4	5781					2	1	4
Mc Naughton, N.	O7	35	7	Q1	974							1
Mc Neil, D.A.C.	L6	5	6	I1	4212							1
Mead, C.J.	T2	21	6	B17	680		1	1	1			6
Mead, C.J.	T2	21	6	B17	681							
Mead, C.J.*	T2	21	6	B17	682							
Meese, G.B.	C1	4	7	A12	100							9
Mello, G.D.D'	B26	35	7	N7	5504				1	3		5
Messenger, J.B.*	S11	32	1	S4	3499							4
Michie, W.	A9	39	6	A14	5728					2	1	4
Millar, J.	L27	33	7	P22	2113							1
Miller, J.A.	E8	9	3	H2	4611		1					2
Miller, P.L.*	O10	12	3	E5	3039					1		3

Miller, P.L.*	O10	22	3	P5	3305							
Milne, J.A.	P1	39	7	G4	1157							1
Milner, A.D.	S2	33	7	J11	5375							5
Minton, C.D.T.	P9	5	6	W1	2611				1	1	2	5
Mitson, R.B.*	L75	38	5	B18	3820							1
Moleman, P.	L15	30	7	P7	3480							1
Moller, T.H.	I1	28	2	B18	3399		1				1	4
Moller, T.H.	I1	22	2	M4	5101							
Monaghan, P.*	G4	5	6	I1	1363					1		3
Monaghan, P.*	G4	8	6	A12	4497							
Montgomery, W.I.*	B12	9	7	J38	4683						1	2
Moore, M.J.*	A5	32	2	J16	3502							1
Morgan, E.	B25	28	2	A12	778						2	5
Morgan, E.	B25	28	2	A12	779							
Morgan, E.	B25	28	2	B18	3406							
Morgan, E.D.	K1	1	3	P5	1226				1	1	2	5
Morgan, M.A.	C23	30	4	G1	824							2
Morgan, M.A.	C23	36	7	P22	5574							
Morgan, M.J.	D6	17	7	L3	544	2	3	6	4	3	3	24
Morgan, M.J.*	D4	27	1	B18	3373							
Morgan, M.J.	D6	33	7	Q1	5390							
Morgan, S.	L44	33	7	B7	5377							1
Morinan, A.	L51	13	7	P7	4855						1	2
Morris, R.C.	P4	17	7	P17	4886				2	1		4
Morris, R.G.M.*	S2	18	1	Q1	1794		3	2	2		1	9
Morton, A.C.*	P9	1	3	E6	3956							1
Morton, M.C.	S2	33	7	J11	5375							1
Mosely, S.	D2	8	6	J3	299							1
Moss, D.	A1	5	6	J7	4226				1			2
Moss, R.	L30	1	6	I1	39							4
Moss, R.	L30	3	6	O4	1315							
Mumford, L.	L51	35	7	P22	973					2		4
Mumford, L.	L51	35	7	P22	3690							
Muntz, W.R.A.	S27	24	6	B12	5131							4
Nadel, L.	L58	37	1	P14	5619			3			1	5
Nash, R.D.M.	M13	28	5	B18	3432							1
Nast, F.*	N11	9	2	M8	2860							1
Naylor, E.	I1	28	2	B18	3404							8
Naylor, E.	I1	22	2	M4	5101							
Newton, I.	A1	5	6	J7	4226	1	2	1	1	1	1	8
Nicholas, D.J.	D6	17	7	L3	844			3				4
Nieto, J.	S29	17	7	P7	3148							1
Norris, M.L.	C1	13	7	L1	479							3
North, E.*	M3	2	5	J20	2480							1
Nowell, N.W.	H10	36	7	J14	2215							19
Oakley, D.A.	L63	33	7	B21	908							17
Oakley, D.A.*	L63	33	1	T2	2099							
Oakley, D.A.*	L63	11	1	B18	3015							
Oakley, D.A.	L44	33	7	B7	5377							
Oakley, D.A.*	L63	33	7	P7	5405							
Oakley, S.G.*	I1	28	2	B18	3407							1
O'Connor, R.J.*	D7	8	7	A12	2824		1		1	1		5
O'Connor, R.J.	D7	8	7	A12	2826							
Odling-Smee, F.J.	L63	37	1	A7	3769					1	1	4

Odling-Smee, F.J.	L56	18	7	P7	4979							
O'Donald, P.*	C9	37	1	T1	5608		1	2		4	2	10
O'Hare, P.J.	L30	3	6	O5	2518							1
O'Keefe, J.	L58	37	1	P14	5619			2		1	1	5
Oliver, G.W.O.	P7	19	7	G2	5020							2
Oliver, J.I.	C12	4	8	A12	103						1	2
Olson, C.R.	C10	24	7	E10	5140							1
Orlove, M.J.*	S29	11	3	S6	1643			1				2
Ostwald, R.	M5	13	7	D2	505							1
Owen, M.	S12	3	6	W1	2521							5
Owens, R.G.	O19	38	1	B3	1094							1
Parish, T.	L30	8	7	J7	2823							1
Parker, A.*	S6	6	6	B25	1380							1
Parker, A.G.	C21	5	4	J3	4200							1
Parker, D.M.	A6	33	6	B12	3531			1		1		3
Parker, G.A.*	L9	5	1	B18	1330	3		2	1	1	1	14
Parker, G.A.*	L9	11	1	B18	1633							
Parker, G.A.	M9	11	6	R8	1657							
Parker, G.A.	C12	37	1	N2	2239							
Parker, G.A.	E12	37	1	A12	2243							
Parker, G.A.	L9	37	1	A12	3762							
Parr, M.	S4	9	3	O1	1538	1						2
Parr, M.J.	S4	9	3	O1	1538	1					1	3
Parr, R.*	L30	5	6	E25	2616							1
Parrot, R.F.	C1	34	7	P7	930			3	2	1	2	9
Parry, K.	K1	1	3	P5	1226						1	2
Partridge, L.*	E8	9	1	B18	1509	1		3			1	7
Partridge, L.*	E8	11	3	N2	4755							
Patterson, I.J.	A4	7	6	A12	212				1	1		3
Patton, S.	P4	25	3	E2	744							1
Paul, D.H.	M7	32	5	J13	3510	1	1					3
Pavey, J.	N14	4	2	A12	94						1	2
Payne, A.P.*	G2	1	7	A12	53							14
Pearce, J.M.	C8	17	7	A15	4916		1	1		1	4	9
Pearce, J.M.	C8	18	7	Q1	4956							
Penett, D.	O7	32	8	B21	2095							1
Pennington, B.J.*	P9	13	2	B24	3059							1
Perrins, C.M.	O13	11	6	A12	442						2	5
Perrins, C.M.	O13	5	6	O4	1355							
Perrins, C.M.	N11	9	6	B18	2942							
Perry, G.C.	B9	1	7	J9	2452	1		1				3
Peterson, E.L.*	S29	28	3	B9	5232							1
Phillips, K.C.	H9	18	7	P23	4950			2				3
Picard, R.S.	C20	38	3	B3	3813			1				2
Pickett, J.A.	H2	1	3	P5	2408							1
Pickstock, J.C.	B3	1	6	J2	4012							1
Pienkowski, M.W.	D7	21	6	B17	1917			2	1	1		6
Pienkowski, M.W.	D7	5	6	L5	2603							
Plotkin, H.C.*	L63	19	3	A12	605	1	3		2			10
Plotkin, H.C.*	L63	11	1	B18	3016							
Plotkin, H.C.	L63	37	1	A7	3769							
Plotkin, H.C.	L44	33	7	B7	5377							
Pope, G.S.	R2	39	7	A20	3859							1
Pope, S.G.	S10	33	7	B5	5374							1

Popham, E.J.	S4	8	3	O1	2740						3	4
Posadas-Andrews, A.	B24	35	6	P22	2156					1		2
Powell, A.J.	H6	1	7	B5	2456							1
Priede, I.G.*	A7	28	5	B18	3435				1		1	3
Puerto, A.	O7	32	8	B21	2095			3	1	1		6
Pullin, R.S.V.	I1	28	2	B18	3404							2
Pullin, R.S.V.	M13	28	5	B18	3432							
Pycock, C.J.	B33	33	7	N4	2114				3	2	1	7
Quicke, D.L.J.	N14	4	2	A12	94							1
Rainey, R.C.*	P9	9	3	M9	2900		1					3
Rainey, R.C.*	N11	21	3	P10	5059							
Raisman, G.	L31	33	7	B21	897							3
Rankin, A.	E4	8	2	P13	240							1
Ratcliffe, P.R.	G5	8	6	J38	4471							1
Rawlins, J.N.P.	O7	33	7	E10	5389							2
Rawlins, J.N.P.	O7	38	7	P7	5711							
Redfern, P.H.	B7	18	7	J32	577							8
Redgrave, P.	H9	35	7	L4	2139			1	3		1	6
Reese, B.	S27	17	7	Q1	563							1
Rentmore, G.	L54	38	7	J38	5694							1
Retter, W.C.	N11	39	7	G4	3873							1
Reynolds, J.	C6	25	7	J34	1971							1
Ridgers, A.	B10	17	7	P16	4924	1						2
Ridley, M.	O12	11	2	Z1	4748						1	2
Ridley, R.M.	H4	35	8	B15	2196							14
Ridley, R.M.	H4	35	8	P22	3708							
Ridley, R.M.	H4	19	8	P22	5010							
Robbins, T.W.	C8	33	7	N2	5393							15
Roberts, A.M.	O3	21	2	A4	3249							1
Roberts, B.L.	M7	32	5	J13	3510							1
Roberts, C.D.*	B14	3	2	S6	2499							1
Roberts, D.M.	D7	28	3	J28	5226				1			2
Roberts, J.	L34	37	1	A12	3754							1
Rodgers, J.R.	B28	35	7	P22	2189							1
Rodgers, R.J.	L56	35	7	P4	3631				1	3	1	9
Rodgers, R.J.	B28	35	7	P4	3632							
Rodgers, R.J.*	B28	30	1	B18	5281							
Rodgers, R.J.*	B28	35	7	P22	5539							
Rolls, E.T.	O7	32	8	B21	2095							26
Roper, R.	C12	38	1	B9	2288			1				2
Roper, T.J.	S29	17	7	P7	3148	1	1	1	4	1	4	14
Roper, T.J.*	S29	17	7	Q1	4913							
Roper-Hall, A.	O7	32	8	B21	2095						1	2
Rose, F.D.	L44	33	7	B7	5377				1			2
Rose, G.P.	P7	19	7	G2	5020							1
Rose, S.P.R.	M15	30	6	N9	5287							8
Rosett, R.E.	M5	13	7	D2	505							1
Rothwell, N.J.	L37	27	7	J11	5202							1
Rowe, J.J.	G5	8	6	J38	4471							1
Russell, I.S.	L63	33	7	B21	908							13
Russell, I.S.*	L67	38	1	P7	3805							
Russell, P.A.	A3	25	7	A15	1974							9
Russell, P.A.*	A6	40	1	B18	2351							

Russell, S.*	L63	30	1	B18	3471							1
Rutter, M.*	L51	6	8	C4	1392							1
Ryland, J.S.*	S31	32	2	S6	3504			1				2
Sahgal, A.	N2	36	6	C6	3720			3	1	1	4	11
Sahgal, A.*	N2	32	1	T2	5319							
Salzen, E.A.*	A6	40	1	V18	2352			1		2		5
Salzen, E.A.	A6	33	6	B12	3531							
Sanger, D.J.	C19	27	7	P4	767	1	1	6	5	2	4	22
Sanger, D.J.*	C19	17	7	P4	3150							
Sanger, D.J.*	C19	17	7	P16	4925							
Sangster, G.I.	A2	22	2	P13	695							1
Saunders, T.S.	B3	2	3	A12	1279							1
Savage, A.A.*	C28	5	3	A21	4160							1
Savory, C.J.*	E3	8	6	A12	2814			1		3	2	8
Savory, C.J.*	E3	28	6	A20	3445							
Sayers, Z.	O3	21	2	A4	3249							1
Schnieden, H.	M6	35	7	P4	1010					2		3
Schofield, C.J.*	L28	12	3	B34	3035					2		3
Scholes, P.	L75	21	5	J1	1904							1
Schoot, P. van der	L15	30	7	P7	3480							1
Scott, P.D.*	N5	37	1	J37	3765							2
Scott, P.D.*	N5	37	1	J37	3766							
Scraggs, P.R.	H4	35	8	B15	2196						1	3
Scraggs, P.R.	H4	35	8	P22	3708							
Seeherman, H.J.	C2	22	1	N2	3294							1
Sewell, R.D.E.	P5	35	7	J32	5537							1
Shaw, G.*	P9	7	6	B17	1411						1	2
Shelton, G.A.B.	O10	32	2	S6	3505			1				2
Sherwood, M.R.C.	L31	33	7	B21	897							1
Simmonds, K.E.L.*	L5	40	6	B25	3896							5
Simpson, J.*	H2	1	3	J5	3976	2	2					5
Simpson, M.J.A.	C16	5	8	L1	188			1	1	1		6
Simpson, M.J.A.*	C16	6	8	A12	200							
Simpson, M.J.A.	C16	6	8	B9	4302							
Skinner, G.J.*	L1	3	3	J3	4085							2
Skinner, G.J.*	L1	8	3	J3	4443							
Slater, F.M.	C21	5	4	J3	4200							1
Slater, P.J.B.*	S29	37	1	T2	2246							12
Slater, P.J.B.	S28	1	6	B9	2247							
Sloan, N.A.*	L53	9	2	E9	1512							1
Sluckin, W.	L5	13	6	Q1	4815							1
Sly, J.	L55	33	7	P7	5410						1	2
Smart, J.L.*	M5	13	1	B18	4806	3	4	2	2	4	3	20
Smart, J.L.	M5	13	7	P7	4868							
Smith, G.	I1	28	2	B18	3404							1
Smith, J.M.*	S29	5	1	B18	1328							5
Smith, R.H.*	R4	11	7	H2	3026		1				2	4
Smyly, W.J.P.*	A12	8	3	H4	4440							1
Solomon, M.E.	B38	8	6	J7	304							1
Somerville, S.H.	E9	39	7	A20	1167							1
Sotthibandhu, S.	M9	21	3	A12	670							1
Southwood, T.R.E.	L49	8	3	A18	1444						1	2
Spellenberg, I.F.	S15	9	4	O2	4630					1		2

Spencer, P.T.	B4	17	1	J36	1750						1	2
Spencer, R.	T2	21	6	R5	5083							3
Spiteri, N.J.	D6	5	7	P7	2627							1
Steel, E.*	C16	5	7	A12	184							11
Steel, E.*	C16	5	7	A12	2636							
Stein, D.G.	C8	35	7	B21	3633	1	2		2	1	3	10
Stephens, D.N.	L30	34	7	E7	942			4	3			8
Stephenson, J.W.*	H2	25	2	J27	3342			1				2
Stevenson-Hinde, J.	C16	6	8	A12	2671							5
Stillwell-Barnes, R.	C16	6	8	A12	2671							1
Stinus, L.	C8	34	7	N11	1965		2		1	2		6
Stock, M.J.	L37	27	7	J11	5202							1
Stoddart, D.M.*	N11	9	1	B18	2849	1			1	1		4
Stolerman, I.P.	B26	35	7	N7	5504							12
Stutt, I.	S3	25	2	M3	5152							1
Summers, D.D.B.*	W4	9	6	B25	1560							1
Suttie, J.M.*	B39	4	7	J38	4118							1
Sweeney, K.F.	B24	35	7	P22	1016						2	3
Swift, S.M.*	A7	28	7	J38	5246							1
Sykes, A.H.	L70	39	6	B31	5734							1
Taberner, P.V.	B33	38	7	P7	5710							1
Taleisnik, S.	L31	33	7	B21	897							1
Tanner, T.*	C22	35	7	N7	992					1		2
Taylor, G.K.*	S2	8	6	I1	4490							1
Taylor, I.R.*	E6	8	6	O5	310							2
Tatlor, I.R.*	E6	8	6	I1	1482							
Taylor, L.R.	N11	9	1	B18	2848	2	1			1	1	7
Taylor, L.R.	H2	9	3	J3	2883							
Taylor, P.J.	S15	9	4	O2	4630							1
Taylor, R.A.J.*	L46	21	3	J3	668							3
Taylor, R.A.J.	N11	9	1	B18	2848							
Taylor, R.A.J.	H2	9	3	J3	2883							
Taylor, R.C.*	C25	21	6	O5	5075							1
Teixeira, A.R.	L51	35	7	P22	973					2		3
Thexton, A.J.	L38	13	7	B21	507	1						2
Thomas, G.V.	S19	19	7	J18	1850	1	1					3
Thomas, K.V.	A15	35	7	P22	2165						2	3
Thompson, D.J.	O12	11	2	Z1	4748						1	2
Thomson, R.*	L5	40	1	B18	2347		3				1	5
Thornton, E.W.	L8	30	7	P22	832	2		2			1	6
Thorpe, S.J.	O7	32	8	B21	2095							1
Tittmar, H.- G.	B13	37	1	V1	2237							1
Toates, F.M.	B24	35	7	P22	1016							12
Toates, F.M.*	M14	8	1	B4	1432							
Toates, F.M.	M14	8	6	A12	1478							
Toates, F.M.*	M14	27	1	B18	5193							
Toosey, F.M.	C1	13	6	B9	4817							1
Townsend, C.R.	N10	9	3	J3	2889	3	3				1	9
Townsend, C.R.	N10	2	2	O2	4043							
Treisman, M.*	O7	1	6	A12	2432							8
Trimnell, L.E.	N2	36	6	C6	3720							1
Tsacas, L.	O10	1	3	A12	2395							1

Tweed, R.L.	L35	38	1	A12	2271							1
Tye, N.C.	W2	35	7	N7	2168							7
Tyler, S.J.*	K2	38	1	A12	1115							4
Tyler, S.J.*	P9	8	6	B25	2811							
Tyler, S.J.*	P9	21	6	R5	3266							
Vince, M.A.*	C1	13	7	A12	503			1	1	1		5
Vince, M.A.	C1	13	6	B9	4817							
Waage, J.K.*	L49	9	3	J3	1531	1				1	2	5
Waber, E.S.*	C1	39	7	A20	5769							1
Wadhams, L.J.	S26	1	3	E3	14						1	2
Walser, E.S.*	C1	6	1	M7	1373						1	2
Warner, G.F.*	R4	3	2	S6	2494		1					2
Watson, A.	L30	3	6	O4	1315		1			1	2	6
Watson, A.	L30	3	6	O5	2518							
Watson, J.*	A4	9	6	B17	2947							1
Watson, J.N.	N11	39	7	G4	3873							1
Watts, F.N.*	L24	15	1	P14	517							1
Wearden, J.H.*	M8	17	7	J36	1780							3
Wearden, J.H.	M8	17	7	J36	3158							
Wearden, J.H.*	M8	19	1	J36	4990							
Webb, L.	B12	9	2	A12	1511							1
Weight, M.L.	H4	19	8	P22	5010							1
Wells, R.	S12	3	6	W1	2521			1				2
Wendlandt, S.	L31	33	7	B5	3567							1
Wenham, M.J.	S26	1	3	E3	14						1	2
Whiton, A.*	S2	21	6	A12	3277							1
Will, B.E.	D6	33	7	Q1	5390			1	5	2		9
Williams, B.G.	I1	28	2	B18	3404						1	2
Williams, J.A.*	I1	28	2	B18	3401							2
Williams, J.A.	I1	28	2	B18	3404							
Williamson, A.J.	A6	33	6	B12	3531			1		1		3
Willner, J.	L58	37	1	P14	5619							1
Wilson, C.J.	L30	9	7	J7	4696	1		1				3
Wilson, J.F.	C23	30	4	G1	824	1					1	4
Wilson, J.F.	C23	36	7	P22	5574							
Winder, M.	H2	1	3	P5	2408							1
Winn, P.	H9	35	7	L4	2139							1
Woiwod, I.P.	H2	9	3	J3	2883						1	2
Wolff, P.R.	H6	1	7	B5	2456							1
Woodhead, S.	L14	8	3	B14	2765							1
Wookey, P.E.	P4	17	7	P17	4886							8
Wotton, R.S.*	L44	8	3	O3	4447							1
Wren, A.	M6	35	7	P4	1010					3		4
Wynne-Edwards, V.C.*	N11	9	1	B18	2847							1
Yates, C.A.	C6	28	7	B21	3451							1
Young, J.O.	L9	8	2	H4	4388							1
Young, J.Z.*	L71	17	1	R10	3131		2					3
Young, M.	C12	38	1	B9	2288							2
Young, M.	C12	13	7	B5	3087							
Zeki, S.*	L58	24	8	N2	5142							1
Zunz, M.	C16	6	8	A12	2671							1

APPENDIX VII

Keys to codes used in Appendices I, IV, V & VI.

Category 1: Work base, as quoted in abstracts and articles and with total numbers of author attributions for the four periods - a. Code used b. Work base c. Totals for 1938-59 d. Totals for 1973 e. Totals for 1974-9 f. Totals for 1980.

a	b	c	d	e	f
A1	Nature Conservancy Council / Institute of Terrestrial Ecology, Monk's Wood Experimental Station, Abbots Ripton, Huntingdon, Cambridge	0	7	0	4
A2	Marine Laboratory, Department of Agriculture and Fisheries for Scotland, Aberdeen	0	1	0	4
A3	University of Aberdeen	0	2	0	2
A4	Culterty Field Station, University of Aberdeen	0	0	0	4
A5	Department of Anatomy, University of Aberdeen	0	0	0	1
A6	Department of Psychology, University of Aberdeen	1	3	0	5
A7	Department of Zoology, University of Aberdeen	0	0	0	8
A8	Natural Environment Research Council Fish Biochemistry Research Unit, University of Aberdeen	0	1	0	0
A9	North of Scotland College of Agriculture, Bee Research Department, Marischal College, University of Aberdeen	8	0	0	2
A10	Department of Animal Health, University College of Wales, Aberystwyth	1	0	0	0
A11	Department of Zoology, University College of Wales, Aberystwyth	1	1	13	1

A12	Freshwater Biology Asociation, Ambleside, Cumbria	0	0	0	1
A13	Natural Environment Research Council Unit for Marine Invertebrate Biology, Marine Science Laboratory, Menai Bridge, Anglesey	0	0	0	2
A14	Department of Biological Science, University of Aston	0	0	0	1
A15	Pharmacology Laborarory, Department of Pharmacy, University of Aston	0	0	0	2
A16	Hannah Research Institute, Department of Agriculture and Fisheries for Scotland, Ayr	0	0	0	1
B1	Nature Conservancy Council / Institute of Terrestrial Ecology Research Station, Banchory	0	3	0	1
B2	Nature Conservancy Council / Institute of Terrestrial Ecology Research Station, Bangor	0	1	0	0
B3	Department of Applied Zoology, University College of North Wales, Bangor	0	2	1	8
B4	Department of Psychology, University College of North Wales, Bangor	0	0	15	3
B5	Marine Biological Station, University College of North Wales, Bangor	1	0	0	0
B6	School of Plant Biology, University College of North Wales, Bangor	0	2	0	0
B7	Pharmacology Group, School of Pharmacy, University of Bath	0	3	0	2
B8	School of Biological Sciences, University of Bath	0	2	0	0
B9	Primate Behaviour Research Laboratories, Institute of Psychiatry, Bethlem Royal Hospital, Beckenham, Kent	0	4	0	2
B10	New University, Ulster, Belfast	0	0	0	5
B11	Department of Psychology, Queen's University, Belfast	0	2	6	3

B12	Department of Zoology, Queen's University, Belfast	0	0	1	5
B13	School of Psychology, Ulster College, Jordanstown, Belfast	0	0	0	1
B14	Department of Botany and Zoology, Ulster Museum, Belfast	0	0	0	1
B15	School of Psychology, Ulster Polytechnic, Belfast	0	0	0	2
B16	Veterinary Research Laboratory, Stormont, Belfast	0	0	0	2
B17	Ethology Laboratory, Uffculme Clinic, Birmingham	0	0	6	0
B18	University of Birmingham	3	0	1	1
B19	Department of Anatomy, Medical School, University of Birmingham	7	12	9	0
B20	Department of Medicine, Queen Elizabeth Hospital, University of Birmingham	0	0	1	0
B21	Department of Pharmacology, University of Birmingham	9	0	0	0
B22	Department of Physiology, Medical School, University of Birmingham	0	0	0	1
B23	Department of Psychiatry, Sub-Department of Ethology, Medical School, University of Birmingham	0	0	18	0
B24	Department of Psychology, University of Birmingham	0	10	46	18
B25	Department of Zoology and Comparative Physiology, University of Birmingham	1	0	0	6
B26	Medical Research Council Neuropharmacology Unit, Medical School, University of Birmingham	0	0	8	4
B27	Neurocommunications Research Unit, University of Birmingham	0	4	0	0
B28	Postgraduate School of Psychology University of Bradford	0	0	0	6

B29	Postgraduate School of Studies in Pharmacology, University of Bradford	0	2	22	0
B30	Brunel Technical College, Bristol	0	1	0	0
B31	University of Bristol	0	0	0	1
B32	Department of Anatomy, Medical School, University of Bristol	0	0	3	0
B33	Department of Pharmacology, Medical School, University of Bristol	0	3	0	5
B34	Department of Physiology, University of Bristol	0	1	0	0
B35	Department of Psychology, University of Bristol	0	1	1	0
B36	Department of Veterinary Medicine / School of Veterinary Science, University of Bristol	1	4	0	0
B37	Department of Zoology, University of Bristol	3	2	0	0
B38	Long Ashton Research Station, University of Bristol	0	0	0	2
B39	Rowett Institute of Research in Animal Nutrition, Bucksburn, Aberdeenshire	4	0	0	1
B40	Ministry of Agriculture, Fisheries and Food, Fisheries Laboratory, Burnham on Crouch	0	0	0	2
C1	Agricultural Research Council Institute of Animal Physiology, Babraham, Cambridge	2	10	27	15
C2	Natural Environment Research Council Sea Mammal Research Unit, c/o British Antarctic Survey, Madingley Road, Cambridge	0	0	0	2
C3	University of Cambridge	2	0	0	1
C4	Agricultural Research Council Unit for Reproductive Physiology and Biochemistry, University of Cambridge	0	4	0	0

C5	Botanic Gardens, University of Cambridge	0	1	0	0
C6	Department of Anatomy, University of Cambridge	0	7	29	6
C7	Department of Applied Mathematics and Theoretical Physics, University of Cambridge	0	1	0	1
C8	Department of Experimental Psychology, University of Cambridge	1	6	87	17
C9	Department of Genetics, University of Cambridge	0	0	0	1
C10	Physiology Laboratory, University of Cambridge	0	2	9	5
C11	Department of Zoology, University of Cambridge	0	4	2	11
C12	Department of Zoology, Sub-Department of Animal Behaviour / Ornithological Field Station, University of Cambridge, Madingley	36	19	17	13
C13	Department of Zoology, Sub-Department of Entomology, University of Cambridge	2	0	0	0
C14	King's College Research Centre, University of Cambridge	0	0	0	12
C15	Medical Research Council Neurochemistry and Pharmacology Unit, Medical School, University of Cambridge	0	3	0	0
C16	Medical Research Council Unit for the Development and Integration of Behaviour, University of Cambridge, Madingley	0	8	23	12
C17	University College, Cardiff	0	4	0	1
C18	Department of Chemistry, University College, Cardiff	0	2	0	0
C19	Department of Psychology, University College, Cardiff	0	1	7	6
C20	Department of Zoology, University College, Cardiff	0	4	0	2

C21	Department of Applied Biology, University of Wales Institute of Science and Technology, Cardiff	0	0	0	3
C22	Department of Applied Pharmacology, Welsh School of Pharmacy, University of Wales Institute of Science and Technology, Cardiff	0	0	0	1
C23	Department of Pharmacology, Welsh National School of Medicine, Cardiff	0	0	0	4
C24	Cheltenham College, Gloucester	0	2	0	0
C25	Chew Valley School	0	0	0	1
C26	Fisheries Research Laboratory, Coleraine	0	1	0	0
C27	Agricultural Research Council Field Station, Compton, Berkshire	1	0	0	0
C28	Crewe and Alsager College of Higher Education	0	0	0	1
C29	I.C.I. Healey Manor Farm, Crewkerne, Somerset	1	0	0	0
D1	Scottish Horticultural Research Institute, Dundee	0	0	0	1
D2	Department of Biological Science / Natural History, University of Dundee	1	2	0	5
D3	Department of Psychology, University of Dundee	0	1	0	0
D4	University of Durham	0	0	1	1
D5	Department of Extra-Mural Studies, University of Durham	0	0	0	3
D6	Department of Psychology, University of Durham	2	7	15	7
D7	Department of Zoology, University of Durham	0	0	0	11
E1	Rentokil Ltd, East Grinstead	0	1	0	0
E2	Agricultural Research Council Animal Breeding Research Organization, Edinburgh	1	1	0	0

E3	Agricultural Research Council Poultry Research Centre, Edinburgh	8	18	50	9
E4	Diving Science Unit, Department of Brewing and Biological Science, Heriot-Watt University, Edinburgh	0	0	0	3
E5	University of Edinburgh	1	0	0	0
E6	Department of Forestry and Natural Resources, University of Edinburgh	0	0	0	2
E7	Department of Psychiatry, Royal Edinburgh Hospital, University of Edinburgh	0	1	0	0
E8	Department of Zoology, University of Edinburgh	6	5	0	4
E9	School of Agriculture, University of Edinburgh	0	0	0	2
E10	Department of Zoology, University College of the South West, Exeter	1	0	0	0
E11	University of Exeter	1	6	0	0
E12	Department of Biological Science, University of Exeter	0	0	0	3
E13	Department of Psychology, University of Exeter	0	2	0	1
G1	Department of Biological Science, Glasgow College of Technology	0	0	6	5
G2	Department of Anatomy, University of Glasgow	0	0	9	1
G3	Department of Chemistry, University of Glasgow	0	3	0	0
G4	Department of Zoology, University of Glasgow	4	5	0	3
G5	Forestry Commission, Glenbrowter	0	0	0	2
G6	B.D.H.(Research) Ltd, Godalming	0	1	0	0
G7	Glaxo Laboratories Ltd, Greenford, Middlesex	1	0	0	0

H1	Ministry of Agriculture, Fisheries and Food Plant Pathology Laboratory, Harpenden	0	1	0	0
H2	Rothamsted Experimental Station / Bee Research Department, Harpenden	22	11	6	15
H3	Department of Neuropharmacology, Tobacco Research Council Laboratories, Harrogate	0	2	0	0
H4	Division of Psychiatry, Clinical Research Centre, Northwick Park Hospital, Harrow, Middlesex	0	0	3	9
H5	Avicultural Society, High Wycombe	0	1	0	0
H6	Division of Life Sciences, Huddersfield Polytechnic	0	0	0	2
H7	Pharmaceutical Research Laboratory, Pharmaceutical Division, Reckitt and Coleman, Hull	0	2	0	0
H8	University of Hull	0	2	0	0
H9	Department of Psychology, University of Hull	0	9	8	5
H10	Department of Zoology, University of Hull	1	6	23	2
I1	Marine Biological Station, University of Liverpool, Port Erin, Isle of Man	0	3	0	10
K1	Department of Chemistry, University of Keele	0	0	0	2
K2	Department of Psychology, University of Keele	0	0	1	1
L1	Department of Biological Science, University of Lancaster	0	0	0	2
L2	Department of Politics, University of Lancaster	0	0	0	1
L3	Department of Psychology, University of Lancaster	0	0	0	4
L4	Department of Psychology, University of Leeds	0	2	1	6

L5	Department of Psychology, University of Leicester	0	10	0	7
L6	Department of Zoology, University of Leicester	0	0	0	2
L7	Glasshouse Crops Research Institute, Littlehampton	0	0	0	2
L8	Department of Psychology, University of Liverpool	0	0	6	4
L9	Department of Zoology, University of Liverpool	2	1	0	8
L10	Faculty of Veterinary Science, University of Liverpool	0	2	0	0
L11	Unit of Reproductive Biology, University of Liverpool	0	4	0	0
L12	British Museum (Natural History), London	1	0	0	1
L13	Department of Entomology, British Museum (Natural History), London	0	1	0	0
L14	Centre for Overseas Pest Research, London	0	3	0	6
L15	Department of Physiology, Charing Cross Hospital Medical School, London	0	0	0	3
L16	Animal Acoustics Unit, City of London Polytechnic	0	0	0	1
L17	Department of Biological Science, City of London Polytechnic	0	0	0	4
L18	Department of Psychology, City of London Polytechnic	0	6	7	0
L19	Department of Social Science and Humanities, Psychology Division, City University, London	0	0	4	1
L20	Commonwealth Institute of Entomology, London	0	1	0	0
L21	Department of Physiology, Guy's Hospital, London	1	0	0	0

L22	Medical Research Council Vision Research Unit, Institute of Opthalmology, London	1	0	0	0
L23	King's College Hospital Medical School, Denmark Hill, London	0	0	1	0
L24	Department of Clinical Psychology, King's College Hospital, Denmark Hill, London	0	0	0	1
L25	Laboratory Animals Bureau, Medical Research Council Laboratories, Holly Hill, Hampstead, London	1	0	0	0
L26	London Hospital Medical Clubs Union	0	0	0	1
L27	Department of Pharmacology and Therapeutics, London Hospital Medical School	0	0	0	2
L28	London School of Hygiene and Tropical Medicine	0	0	0	3
L29	Ministry of Agriculture, Fisheries and Food Infestation Control Division, London	4	0	0	0
L30	Department of Experimental Psychology, Institute of Neurology, National Hospital, Queen's Square, London	0	5	14	14
L31	National Institute of Medical Research, Mill Hill, London	4	0	0	9
L32	Department of Paramedical Science, North East London Polytechnic	0	0	0	2
L33	Department of Life Science, Polytechnic of Central London	0	1	0	1
L34	Institute of Environmental Science and Technology, Polytechnic of the South Bank, London	0	0	0	3
L35	Neurophysiology Department, Royal Free Hospital, Hampstead, London	0	0	0	2
L36	Department of Pharmacology, Medical College, St Bartholomew's Hospital, London	0	0	0	1

L37	Department of Physiology, St George's Hospital Medical School, London	0	0	0	2
L38	Department of Physiology, Royal Dental Hospital School of Dental Surgery, St George's Hospital Medical School, London	0	0	0	2
L39	University of London	2	0	0	0
L40	Department of Psychology, Bedford College, University of London	1	0	0	0
L41	Department of Zoology, Bedford College, University of London	0	0	0	2
L42	Birkbeck College, University of London	4	0	0	0
L43	Department of Psychology, Birkbeck College, University of London	13	0	0	0
L44	Department of Biological Science, Goldsmith's College, University of London	0	0	0	5
L45	Department of Psychology, Goldsmith's College, University of London	0	0	1	0
L46	Agricultural Research Council Insect Physiology Group, Photoperiod Laboratory, Department of Zoology and Applied Entomology, Imperial College Field Station, University of London, Ascot	0	2	0	5
L47	Applied Geochemistry Research Group, Department of Geology, Imperial College, University of London	0	1	0	0
L48	Department of Zoology, Imperial College, University of London	0	2	0	0
L49	Department of Zoology and Applied Entomology, Imperial College of Science and Technology / Imperial College Field Station, Silwood Park, University of London	5	4	0	3
L50	Department of Zoology, King's College, University of London	0	6	0	0

L51	Department of Neurology, British Postgraduate Medical Federation, University of London Institute of Psychiatry, Maudsley Hospital	6	7	36	11
L52	Queen Mary College, University of London	1	0	0	0
L53	Department of Zoology and Comparative Physiology, Queen Mary College, University of London	2	0	0	2
L54	Department of Zoology, Royal Holloway College, University of London	0	1	0	2
L55	Department of Physiology, Royal Veterinary College, University of London	7	0	0	3
L56	Department of Pharmacology, School of Pharmacy, University of London	0	0	19	14
L57	University College, London	5	0	0	0
L58	Department of Anatomy, University College, London	0	0	0	4
L59	Department of Anthropology, University College, London	0	0	0	1
L60	Department of Biometry, University College, London	5	0	0	0
L61	Department of Biophysics, University College, London	0	3	0	0
L62	Department of Botany and Microbiology, University College, London	0	0	0	3
L63	Department of Psychology, University College, London	9	0	5	10
L64	Department of Zoology, University College, London	4	0	0	0
L65	Galton Laboratory, University College, London	1	0	0	0
L66	Medical Research Council Cerebral Function Group, Department of Anatomy, University College, London	0	2	0	0

L67	Medical Research Council Group for the Experimental Investigation of Behaviour / Unit on Neural Mechanisms of Behaviour, Department of Psychology, University College, London	4	2	15	1
L68	Westfield College, University of London	0	2	0	0
L69	Department of Zoology, Westfield College, University of London	0	0	0	2
L70	Wye College, University of London	0	0	0	2
L71	Wellcome Institute for the History of Medicine, London	0	0	0	1
L72	Zoological Society of London, Regent's Park	1	0	0	0
L73	Wellcome Institute of Comparative Physiology, Zoological Society of London, Regent's Park	0	1	2	1
L74	Meteorological Office, R.A.F. Lossiemouth	0	0	0	1
L75	Ministry of Agriculture, Fisheries and Food, Fish Laboratory, Lowestoft	0	0	0	8
M1	Grassland Research Institute, Maidenhead	0	2	0	0
M2	Malham Tarn Field Centre, nr Settle, Cumbria	0	1	0	0
M3	Area Fish Office, Severn-Trent Water Authority, Malvern	0	0	0	1
M4	University of Manchester	0	0	0	1
M5	Department of Child Health, Medical School, University of Manchester	0	0	17	6
M6	Department of Pharmacology, Materia Medica and Therapeutics, University of Manchester	0	0	0	7
M7	Department of Physiology, University of Manchester	0	0	0	2
M8	Department of Psychology, University of Manchester	0	0	0	5

M9	Department of Zoology, University of Manchester	0	1	0	6
M10	Medical Research Council	1	0	0	0
M11	Animal Studies Department, Pedigree Petfoods Ltd, Melton Mowbray	0	2	0	0
M12	Endocrine Unit, Pedigree Petfoods Ltd, Melton Mowbray	0	2	0	0
M13	University Marine Biology Station, Millport, Isle of Cumbrae	0	0	0	3
M14	Department of Biology, Open University, Milton Keynes	0	0	0	5
M15	Brain Research Group, Department of Biology, Open University, Milton Keynes	0	0	2	3
N1	Agricultural Research Council, Institute of Research in Animal Diseases, Compton Laboratory, Newbury	0	0	0	1
N2	Medical Research Council Neuroendocrinology Unit, Newcastle General Hospital	0	0	0	5
N3	Wellcome Research Laboratory, Department of Medicine, Royal Victoria Infirmary, Newcastle-upon-Tyne	0	0	0	2
N4	School of Agriculture, King's College, Newcastle-upon Tyne / Department of Agricultural Biology, University of Newcastle-upon-Tyne	6	0	0	1
N5	Department of Anatomy, University of Newcastle-upon-Tyne	0	0	0	2
N6	Department of Psychology, University of Newcastle-upon-Tyne	0	1	0	4
N7	Department of Zoology, University of Newcastle-upon-Tyne	0	4	0	2
N8	Seal Hayne Agricultural College, Newton Abbot, Devon	1	0	0	0
N9	Institute of Terrestrial Ecology, Colney Research Station, Norwich	0	0	2	0

N10	School of Biological Sciences, University of East Anglia, Norwich	0	0	0	4
N11	Not stated	2	1	0	18
N12	Department of Physiology and Pharmacology, Medical School, University of Nottingham	0	0	0	2
N13	Department of Psychology, University of Nottingham	0	7	1	0
N14	Department of Zoology, University of Nottingham	2	0	0	8
N15	School of Agriculture, University of Nottingham	0	5	0	0
O1	Dunstaffnage Marine Research Laboratory, Oban	0	3	0	4
O2	Medical Research Council Neuroendocrinology Unit, Oxford	0	5	0	0
O3	Oxford Research Unit, Open University	0	0	0	3
O4	Human Development Research Unit, Park Hospital for Children, Oxford	0	1	0	0
O5	Medical Research Council Unit and University Department of Clinical Pharmacology, Radcliffe Infirmary, Oxford	0	0	13	0
O6	University of Oxford	2	6	1	1
O7	Institute and Department of Experimental Psychology, University of Oxford	17	19	60	27
O8	Department of Human Anatomy, University of Oxford	0	1	0	0
O9	Physiology Laboratory, University of Oxford	2	0	0	0
O10	Department of Zoology, University of Oxford	4	2	2	8
O11	Agricultural Research Council Unit for Insect Physiology, Department of Zoology, University of Oxford	0	1	0	1

O12	Animal Behaviour Research Group, Department of Zoology, University of Oxford	0	1	10	12
O13	Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford	1	2	2	10
O14	Department of Zoology and Comparative Anatomy, University of Oxford	25	0	0	0
O15	Department of Zoology and Comparative Anatomy, University Museum, Oxford	4	0	0	0
O16	Bureau of Animal Population, Department of Zoological Field Studies, University of Oxford	6	0	0	0
O17	Hope Department of Entomology, University of Oxford	2	0	0	0
O18	Somerville College, Oxford	0	0	0	1
O19	Warneford Hospital, Department of Psychiatry, University of Oxford	0	0	0	2
O20	Wolfson College, Oxford	0	0	0	1
P1	Department of Agriculture and Fisheries for Scotland, Hill Farming Research Organization, Penicuik	0	0	0	7
P2	Agricultural Research Council Foot and Mouth Disease Research Station, Pirbright, Surrey	1	0	0	0
P3	Marine Biological Association Laboratory, Plymouth	0	2	0	0
P4	School of Environmental Sciences, Plymouth Polytechnic	0	0	0	8
P5	Department of Applied Pharmacology, Polytechnic of Wales, Pontypridd, Mid-Glamorgan	0	0	0	2
P6	Department of Biological Science, Portsmouth Polytechnic	0	2	0	0
P7	School of Pharmacy, Portsmouth Polytechnic	0	0	0	4
P8	Division of Psychology, Preston Polytechnic	0	0	5	2

P9	Private	4	12	0	26
R1	University of Reading	0	2	0	0
R2	Department of Agriculture, University of Reading	0	2	0	4
R3	Department of Psychology, University of Reading	2	2	0	1
R4	Department of Zoology, University of Reading	0	0	5	9
R5	Horticultural Research Laboratories, University of Reading	0	2	0	0
R6	National Institute for Research in Dairying, Shinfield, University of Reading	2	0	1	0
S1	University of St Andrews	1	0	0	0
S2	Department of Psychology, University of St Andrews	0	2	0	6
S3	Gatty Marine Laboratory, University of St Andrews	0	0	0	2
S4	Department of Biology, University of Salford	0	0	0	4
S5	Chemical Defence Establishment, Porton Down, Salisbury	0	0	2	0
S6	Royal Society for the Protection of Birds, Sandy, Bedfordshire	0	0	0	6
S7	Twigmoor Gull Ponds, nr Scawby, Lincolnshire	1	0	0	0
S8	Department of Control Engineering, University of Sheffield	0	0	0	1
S9	Department of Genetics, University of Sheffield	0	2	7	2
S10	Department of Psychology, University of Sheffield	0	4	9	3
S11	Department of Zoology, University of Sheffield	0	2	0	2
S12	Wildfowl Trust, Slimbridge	2	1	0	3

S13	Commonwealth Institute of Biological Control, Ministry of Agriculture, Fisheries and Food Research Laboratory, Slough	0	0	0	1
S14	Chemical Entomology Unit, Department of Biology and Chemistry, University of Southampton	0	0	10	11
S15	Department of Biology, University of Southampton	0	0	7	3
S16	Department of Chemistry, University of Southampton	0	0	6	0
S17	Department of Physiology and Biochemistry, University of Southampton	3	2	0	0
S18	Department of Psychology, University of Southampton	0	1	0	0
S19	Department of Psychology, University of Stirling	0	3	1	4
S20	Psychology Primate Unit, Department of Psychology, University of Stirling	0	3	9	2
S21	Grassland Research Station, Stratford-on-Avon	1	0	0	0
S22	Department of Applied Physiology, University of Strathclyde	0	0	0	1
S23	Milk Marketing Board Cattle Breeding Centre, Sturminster Newton, Dorset	1	0	0	0
S24	Department of Biology, Sunderland Polytechnic	0	0	0	1
S25	University of Sussex	0	0	0	3
S26	Agricultural Research Council Unit for Invertebrate Chemical Physiology, University of Sussex	0	0	0	3
S27	Department / Laboratory of Experimental Psychology, University of Sussex	0	13	37	8

S28	Ethology and Neurophysiology Group, School of Biological Sciences, University of Sussex	0	5	24	9
S29	School of Biological Sciences, University of Sussex	0	8	7	26
S30	Department of Psychology, University College, Swansea	0	0	1	2
S31	Department of Zoology, University College, Swansea	0	3	13	18
T1	Ministry of Agriculture, Fisheries and Food Research Laboratory, Tolworth, Surrey	1	0	0	0
T2	British Institute of Ornithology, Tring	0	2	0	7
T3	Sub-department of Ornithology, British Museum (Natural History), Tring	0	1	0	0
W1	Nature Conservancy Council / Institute of Terrestrial Ecology Furzebrook Research Station, Wareham, Dorset	1	0	6	1
W2	Lilly Research Centre Ltd, Windlesham	0	0	0	2
W3	Entomology Department, Ministry of Agriculture, Fisheries and Food, Woodthorne, Wolverhampton	2	0	0	0
W4	Ministry of Agriculture, Fisheries and Food Pest Infestation Control Laboratory, Field Research Station, Worplesdon	0	0	0	3
Y1	Department of Biology, St John's College, York	0	1	0	0
Y2	Department of Biology, University of York	0	7	7	0
Y3	Department of Psychology, University of York	0	0	6	1

Category 2: Fields of interest, with total numbers of author attributions for the four periods (NA = not applicable) - a. Code used b. Field of interest c. Total for 1938-59 d. Total for 1973 e. Total for 1974-9 f. Total for 1980.

a	b	c	d	e	f
1	Communication	10	25	47	43
2	Aggression and Defence	8	20	25	18
3	Social Spacing	10	NA	NA	15
4	Dominance	4	NA	NA	10
5	Sexual and Reproductive Behaviour	48	35	33	49
6	Relationships between Individuals (Parental - Filial Behaviour, etc.)	8	7	22	15
7	Groups and Social Behaviour	27	23	23	20
8	Maintenance Behaviour (Foraging and and Ingestion, etc.)	33	NA	40	69
9	Behavioural Ecology	1	29	7	58
10	Genetics of Behaviour	5	4	18	2
11	Evolution and Survival Value	21	3	3	23
12	Descriptive Studies	3	12	4	4
13	Ontogeny	8	14	63	31
14	Exploration and Play	NA	6	NA	NA
15	Habituation and Extinction	17	7	23	1
16	Conditioning	NA	20	NA	NA
17	Conditioning (Positive Reinforcement)	4	NA	55	31
18	Conditioning (Negative Reinforcement)	0	NA	39	20
19	Perceptual Discrimination and Complex Learning	12	16	56	16
20	Memory	0	NA	2	1
21	Orientation, Navigation and Migration	11	8	1	36
22	Locomotion	6	NA	0	14
23	Effective Stimuli	NA	30	NA	NA
24	Visual Stimulation	6	NA	17	15
25	External Stimulation (Excluding Visual)	14	NA	15	28
26	Electrical Stimulation	NA	4	24	NA
27	Motivation	4	NA	22	8
28	Rhythms	3	10	4	37
29	Sleep	0	NA	0	0
30	Biochemical and Anatomical Correlates	0	5	17	22
31	Physiological Correlates	NA	24	25	NA
32	Neurophysiological Correlates	17	NA	NA	18
33	Brain Lesions	6	27	57	48
34	Brain Stimulation (Electrical)	0	NA	NA	12
35	Chemical Stimulation and Drugs	9	46	121	84
36	Hormones	5	32	56	28

37	Theoretical Models and Overviews	0	5	11	28
38	Methodology	14	22	23	29
39	Applied Ethology	0	NA	NA	28
40	Miscellaneous	0	28	8	14

Category 3: Animals used, with total numbers of author attributions for the four periods - a. Code used b. Type of animal c. Total for 1938-59 d. Total for 1973 e. Total for 1974-9 f. Total for 1980.

a	b	c	d	e	f
1	General	3	17	39	105
2	Invertebrates (excluding Insects)	11	27	3	68
3	Insects	78	63	48	122
4	Vertebrates (excluding Fish, Birds and Mammals)	6	1	0	18
5	Fish	15	11	0	28
6	Birds	67	114	146	172
7	Mammals (excluding Primates)	132	198	513	325
8	Primates	3	30	111	41

Category 4: Journal in which paper published, with total numbers of different papers per journal for the four periods. Totals are corrected for joint authorships. Key: a. Code used b. Title of journal c. Country of publication (coded according to U.S. Library of Congress MARC II format, 1972) d. Totals for 1938-59 e. Totals for 1973 f. Totals for 1974-9 g. Totals for 1980. (Note: * including Proceedings of the Association for the Study of Animal Behaviour that refer to practical work; ** including Behaviour Supplements.)

a	b	c	d	e	f	g
A1	Acarologia	FR	NA	0	0	1
A2	Acrida	FR	NA	0	3	0
A3	Acta Endocrinologica Supplements	DK	NA	1	0	1
A4	Acta Protozoologica	PL	NA	0	0	1
A5	Activitas Nervosa Superior	CS	NA	0	1	0
A6	Advances in Marine Biology	US	NA	1	0	0
A7	Advances in the Study of Behavior	US	NA	0	4	1
A8	Aggressive Behavior	US	NA	0	4	2
A9	American Journal of Physiology	US	NA	0	2	0
A10	American Naturalist	US	NA	0	0	3
A11	American Psycholgist	US	NA	1	0	0
A12	Animal Behaviour	UK	*44	47	70	54
A13	Animal Behaviour Monographs	UK	NA	1	0	0
A14	Animal Feed Science and Technology	NE	NA	0	0	2
A15	Animal Learning and Behavior	US	NA	0	16	4
A16	Animal Production	UK	NA	1	1	0
A17	Annals of Applied Biology	UK	NA	2	0	3
A18	Annual Review of Ecology and Systematics	US	NA	0	0	1
A19	Annual Review of Psychology	US	NA	0	1	0
A20	Applied Animal Ethology	NE	NA	0	27	6
A21	Archiv fuer Hydrobiologie	GW	NA	0	0	1
A22	Ardea	NE	NA	0	1	0
A23	Association for the Study of Reptilia and Amphibia (ASRA) Journal	UK	NA	0	0	1
A24	Australian Entomological Society Journal	AT	NA	1	0	0
A25	Avicultural Magazine	UK	NA	1	0	1
B1	Bee World	UK	NA	0	2	0
B2	Behavior Genetics	US	NA	0	4	0
B3	Behavior Research Methods and Instrumentation	US	NA	2	0	2
B4	Behavioral and Brain Sciences	UK	NA	0	0	2
B5	Behavioral and Neural Biology	US	NA	0	0	6
B6	Behavioral Biology	US	NA	5	21	1
B7	Behavioral Brain Research	NE	NA	0	0	1
B8	Behavioral Ecology and Sociobiology	US	NA	0	1	0
B9	Behaviour	NE	**71	11	14	10

B10	Behaviour Research and Therapy	US	NA	0	0	1
B11	Behaviour Supplements	NE	NA	8	0	0
B12	Behavioural Processes	NE	NA	0	6	2
B13	Biochemical Society, London, Transactions	UK	NA	0	2	0
B14	Biochemical Systematics and Ecology	US	NA	0	0	1
B15	Biological Psychiatry	US	NA	0	2	1
B16	Biology of Behaviour	FR	NA	0	2	1
B17	Bird Study	UK	NA	4	2	9
B18	(Book)	NA	NA	0	25	78
B19	Brain	UK	NA	0	1	0
B20	Brain, Behavior and Evolution	SZ	NA	0	4	0
B21	Brain Research	NE	NA	9	38	12
B22	Brain Research Bulletin	US	NA	0	1	0
B23	British Antarctic Survey Bulletin	UK	NA	0	0	1
B24	British Arachnological Society Bulletin	UK	NA	0	0	1
B25	British Birds	UK	NA	5	0	9
B26	British Journal of Animal Behaviour	UK	*95	NA	NA	NA
B27	British Journal of Nutrition	UK	NA	0	2	0
B28	British Journal of Pharmacology	UK	NA	0	20	2
B29	British Journal of Psychology	UK	11	4	2	4
B30	British Medical Bulletin	UK	NA	0	1	0
B31	British Poultry Science	UK	NA	2	7	2
B32	British Veterinary Journal	UK	NA	1	2	0
B33	Bulletin of Animal Behaviour	UK	12	NA	NA	NA
B34	Bulletin of Entomological Research	UK	NA	3	0	2
C1	Canadian Journal of Psychology	CN	NA	0	1	0
C2	Canadian Journal of Zoology	CN	NA	2	0	1
C3	Chemical Senses and Flavour	UK	NA	0	2	2
C4	Child Development	US	NA	0	1	1
C5	Coleopterists' Bulletin	US	NA	0	0	1
C6	Communications in Psychopharmacology	??	NA	0	0	1
C7	Comparative and General Pharmacology	US	NA	2	0	0
C8	Condor	US	NA	0	1	0
C9	Crustaceana	NE	NA	0	0	1
D1	Danish Medical Bulletin	DK	NA	1	0	0
D2	Developmental Psychobiology	US	NA	0	12	2
D3	Diseases of the Nervous System	US	NA	1	0	0
E1	Ecological Entomology	UK	NA	0	1	1
E2	Entomologia Experimentalis et Applicata	NE	NA	5	0	4
E3	Entomological Society of America Bulletin	US	NA	0	0	1
E4	Entomologist's Gazette	UK	NA	1	0	1
E5	Entomologist's Monthly Magazine	UK	NA	3	0	8
E6	Entomologist's Record and Journal of Variation	UK	NA	0	0	1
E7	European Journal of Pharmacology	NE	NA	0	8	1
E8	Evolution	US	NA	0	1	0
E9	Experientia	SZ	NA	3	0	2
E10	Experimental Brain Research	US	NA	1	12	3
E11	Experimental Neurology	US	NA	0	4	0

F1	Federation of European Microbiological Societies Microbiology Letters	NE	NA	0	0	1
F2	Folia Primatologica	SZ	NA	0	4	0
F3	Forestry Commission Forest Record	UK	NA	0	0	1
G1	General and Comparative Endocrinology	US	NA	0	0	1
G2	General Pharmacology	US	NA	0	0	1
G3	Genetical Research	UK	NA	0	2	0
G4	Grass and Forage Science	UK	NA	0	0	4
H1	Helgolaender Wissenschaftliche Meeresuntersuchungen	GW	NA	2	0	0
H2	Heredity	UK	NA	0	0	2
H3	Hormones and Behavior	US	NA	3	4	0
H4	Hydrobiologia	NE	NA	0	0	3
I1	Ibis	UK	NA	5	1	10
I2	Insectes Sociaux	FR	NA	1	0	1
I3	International Journal of Neuroscience	UK	NA	0	0	2
I4	International Research Communications System Medical Science: Drug Metabolism and Toxicology	UK	NA	0	0	1
J1	Journal du Conseil Permanent International pour L'Exploration de la Mer	DK	NA	0	0	2
J2	Journal fuer Ornithologie	GW	NA	1	0	1
J3	Journal of Animal Ecology	UK	NA	2	2	11
J4	Journal of Animal Science	US	NA	0	0	1
J5	Journal of Apicultural Research	UK	NA	0	1	2
J6	Journal of Applied Behavioral Science	US	NA	0	1	0
J7	Journal of Applied Ecology	UK	NA	3	3	4
J8	Journal of Arid Environments	UK	NA	0	0	1
J9	Journal of Chemical Ecology	US	NA	0	0	3
J10	Journal of Child Psychology and Psychiatry and Allied Disciplines	US	NA	0	1	0
J11	Journal of Comparative and Physiological Psychology	US	NA	9	20	2
J12	Journal of Comparative Pathology	UK	NA	1	0	0
J13	Journal of Comparative Psychology	US	NA	8	0	9
J14	Journal of Endocrinology	UK	NA	4	14	5
J15	Journal of Entomology (Series A)	UK	NA	1	0	0
J16	Journal of Experimental Biology	UK	NA	2	0	3
J17	Journal of Experimental Marine Biology and Ecology	NE	NA	1	0	0
J18	Journal of Experimental Psychology: Animal Behavior Processes	US	NA	0	5	1
J19	Journal of Experimental Zoology	US	NA	1	0	0
J20	Journal of Fish Biology	UK	NA	1	0	1
J21	Journal of Insect Physiology	US	NA	3	3	0
J22	Journal of Interdisciplinary Cycle Research	NE	NA	1	0	1
J23	Journal of Medical Entomology	US	NA	0	0	1

J24	Journal of Medical Primatology	US	NA	0	1	0
J25	Journal of Medicinal Chemistry	US	NA	0	1	0
J26	Journal of Mental Deficiency Research	UK	NA	0	1	0
J27	Journal of Molluscan Studies	UK	NA	0	0	2
J28	Journal of Natural History	UK	NA	2	0	4
J29	Journal of Neurophysiology	US	NA	4	0	0
J30	Journal of Parasitology	US	NA	1	0	0
J31	Journal of Pharmacology and Experimental Therapeutics	US	NA	0	2	0
J32	Journal of Pharmacy and Pharmacology	UK	NA	0	4	3
J33	Journal of Physiology	UK	NA	0	4	0
J34	Journal of Reproduction and Fertility	UK	NA	4	4	2
J35	Journal of Studies on Alcohol	US	NA	0	0	1
J36	Journal of the Experimental Analysis of Behavior	US	NA	2	20	4
J37	Journal of Theoretical Biology	UK	NA	0	0	4
J38	Journal of Zoology	UK	NA	5	11	8
L1	Laboratory Animals	UK	NA	2	2	2
L2	Laboratory Practice	UK	NA	0	1	0
L3	Learning and Motivation	US	NA	1	7	2
L4	Life Sciences	US	NA	1	4	1
L5	Linnean Society of London: Biological Journal	UK	NA	0	0	3
M1	Malacologia	US	NA	0	0	1
M2	Mammal Review	UK	NA	0	0	1
M3	Marine Behaviour and Physiology	UK	NA	0	0	2
M4	Marine Biological Association of the United Kingdom: Journal	UK	NA	2	1	1
M5	Marine Biology	US	NA	0	0	2
M6	Medical and Biological Illustration	UK	NA	0	1	0
M7	Medical Biology	FI	NA	0	0	1
M8	Meeresforschung / Reports on Marine Research	GW	NA	0	0	1
M9	Mitteilungen der Schweizerischen Entomologischen Gesellschaft	SZ	NA	0	0	1
N1	Natural History	US	NA	1	0	0
N2	Nature	UK	NA	14	19	9
N3	Nature: New Biology	UK	NA	0	1	0
N4	Naunyn-Schmiedeberg's Archives of Pharmacology	US	NA	0	3	1
N5	Nematologica	NE	NA	1	0	0
N6	Neuroendocrinology	SZ	NA	1	0	0
N7	Neuropharmacology	US	NA	2	12	5
N8	Neuropsychologia	US	NA	3	16	1
N9	Neuroscience	US	NA	0	1	1
N10	Neuroscience and Biobehavioral Reviews	US	NA	0	0	1
N11	Neuroscience Letters	IE	NA	0	3	1
N12	New York Academy of Sciences: Annals	US	NA	1	2	1
N13	Norsk Entomologisk Tidsskrift	NO	NA	1	0	0
N14	Nutrition Society: Proceedings	UK	NA	0	1	0
O1	Odonatologica	NE	NA	0	0	2

O2	Oecologia	US	NA	1	0	2
O3	Oikos	DK	NA	0	0	2
O4	Ornis Fennica	FI	NA	0	0	2
O5	Ornis Scandinavica	DK	NA	0	0	6
P1	Pedobiologia	GE	NA	0	0	1
P2	Perception	UK	NA	0	2	0
P3	Pharmacology	SZ	NA	0	1	0
P4	Pharmacology, Biochemistry and Behavior	US	NA	0	36	10
P5	Physiological Entomology	UK	NA	0	3	8
P6	Physiological Psychology	US	NA	2	10	0
P7	Physiology and Behavior	US	NA	18	61	19
P8	Postgraduate Medical Journal	UK	NA	0	1	0
P9	Primates	JA	NA	0	2	0
P10	Proceedings and Transactions: South London Entomological and Natural History Society	UK	NA	0	0	2
P11	Proceedings of the Malacological Society of London	UK	NA	1	0	0
P12	Progress in Neuro-Psychopharmacology	US	NA	0	0	1
P13	Progress in Underwater Science	UK	NA	0	0	2
P14	Psychological Bulletin	US	NA	1	1	2
P15	Psychological Medicine	UK	NA	1	1	0
P16	Psychological Record	US	NA	0	3	2
P17	Psychological Reports	US	NA	3	2	1
P18	Psychological Review	US	NA	0	1	0
P19	Psychonomic Science	US	NA	3	0	0
P20	Psychonomic Society: Bulletin	US	NA	1	3	0
P21	Psychopharmacologia	US	NA	5	20	0
P22	Psychopharmacology	US	NA	0	19	19
P23	Psychophysiology	US	NA	0	0	1
P24	Psychosomatic Medicine	US	NA	0	1	0
Q1	Quarterly Journal of Experimental Psychology	UK	26	10	22	9
R1	Recent Progress in Hormone Research: Proceedings of the Laurentian Hormone Conference	US	NA	1	0	0
R2	Revue du Comportement Animal	FR	NA	4	1	0
R3	Revue Roumaine de Biologie: Serie Biologie Animale	RM	NA	0	0	1
R4	Ricerche di Psicologia	IT	NA	0	0	3
R5	Ringing and Migration	UK	NA	0	0	3
R6	Royal Entomological Society of London: Transactions	UK	NA	1	0	0
R7	Royal Society of Edinburgh, Section B: Proceedings	UK	NA	0	0	1
R8	Royal Society of London, Philosophical Transactions: Series B, Biological Sciences	UK	NA	0	1	1
R9	Royal Society of London, Proceedings: Series B, Biological Sciences	UK	NA	1	0	3
R10	Royal Society of Medicine: Journal	UK	NA	0	0	1
S1	Science	US	NA	1	4	0
S2	Scientific American	US	NA	0	1	0

S3	South African Journal of Psychology	SA	NA	0	0	1
S4	Studies in Biology	UK	NA	0	1	3
S5	(Symposium)	NA	NA	1	4	0
S6	Systematics Association: Special Volumes	US	NA	0	0	9
T1	Theoretical Population Biology	US	NA	0	0	2
T2	Trends in Neurosciences	NE	NA	0	0	4
V1	Verhandlungen der Naturforschenden Gesellschaft in Zurich	SW	NA	0	0	1
V2	Veterinary Record	UK	NA	1	1	1
V3	Vision Research	US	NA	1	0	0
W1	Wildfowl	UK	NA	0	0	4
Z1	Zeitschrift fuer Tierpsychologie	GW	NA	2	2	4
Z2	Zoological Society of London: Symposium	UK	NA	0	1	0

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