

AN EXPERIMENTAL STUDY OF THE COMFORT BEHAVIOUR
OF THE MALLARD (ANAS PLATYRHYNCHOS L.)

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1979

A thesis submitted in accordance with the regulations
for the degree of Doctor of Philosophy at The University
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G.M.C.

CHAPTER ONE

GENERAL INTRODUCTION

1.1 INTRODUCTION

Most animals are faced with the necessity of keeping their body surface in good order - free of soiling matter and of ectoparasites and other organisms - in order that it may function properly. One function of animals' integuments, which is especially important for homiotherms, is the provision of thermal insulation. Subcutaneous tissue, especially fat, contributes to this but, in addition, mammals and birds have outer layers of fur or feathers. Air trapped within this outer structure is responsible for the insulation, and if the complex structure is damaged or distorted, or worse still, if the air spaces become waterlogged, insulation is drastically reduced. In birds, the plumage has another very important function; feathers are primarily an adaptation for flight and their aerodynamic properties are just as important to the characteristic life style of birds as is the insulation function.

Thus feathers, which are rather delicate structures and directly exposed to disruptive effects from the outside world, are of crucial importance to the avian animal. Much of their maintenance is carried out by behavioural means - preening, scratching, shaking and bathing are obvious examples of feather care. Furthermore, while mammals have sebaceous glands widely distributed over the skin secreting substances that assist skin and fur maintenance, birds have only one such gland, the large uropygial gland on the rump, and its secretion "preen-oil" must be transported by behavioural means to the part of the plumage where it is needed - by "oiling" and preening.

If the surmise of ornithologists is correct, the striking activities of anting, sunning (=sunbathing) and dusting (=dustbathing) may also be involved in feather maintenance. The "bare parts" too must be cared for: the bill may be wiped on the substrate or licked with the tongue, and the hind legs "preened" with the bill.

This group of activities, thought to be involved in care of the body surface, is the focus of the present investigation. The subjects are Mallards Anas platyrhynchos which, as water birds where the water repellancy problem is particularly important*, have a rich repertoire of such behaviour (although anting and dusting definitely do not occur). This type of behaviour of ducks and other wildfowl has been scrutinised in far greater detail than for any other group of birds, thanks to the work of McKinney (1965) who drew together previous scattered accounts and supplemented them with many original observations. That account was largely the inspiration for the present study. Throughout this thesis, all undated references to McKinney's work can be taken as referring to this 1965 paper.

The present study is primarily concerned with the causation of behaviour associated with feather care. As well as being of interest in its own right, it will become clear that this has broad implications for our understanding of the motivation of behaviour in general. Hinde (1970) has called for motivational analyses of a far wider range of behaviour than has hitherto been the case, that we may better appreciate the diversity and commonalities of motivational systems. It is toward that end that the present study is aimed.

1.2 SOME TERMINOLOGY - COMFORT BEHAVIOUR

It is useful to have a general term to cover the group of activities outlined above. Hence, in this account, comfort behaviour is to be understood as behaviour obviously directed at the care of the body surface

*Footnote: the role of plumage in waterproofing is illustrated by some measurements reported by Heinroth and Heinroth (1959) on the corpse of a male mallard. With plumage intact, the bird had a specific gravity of 0.65, as opposed to 0.96 when plucked. Air trapped among the feathers is thus very important for floatation.

such as preening and scratching etc., plus shaking, stretching, yawning and some thermo-regulatory movements such as gular fluttering.

Kortlandt (1940) first adopted McDougall's postulate of a comfort instinct to cover this kind of behaviour. Subsequent authors have differed slightly from one another in the scope of their usage of the term. Weidmann (1956), concerned with ducks, excluded bathing and long bouts of oiling-preening, while Simmons (1964), reviewing the type of behaviour considered here for the whole of the class Aves, treated sunning, dusting and anting separately as well. I agree with McKinney (1965) that it is useful to have a general term to cover all of these activities and thus I follow his usage of the term comfort movements: I shall use the term comfort behaviour more or less interchangeably.

Other authors (see McKinney 1965) have used various other generic names for groups of activities including some or all comfort movements. The most common alternative is maintenance activities. This term is usually used for the group of activities such as locomotion, feeding, drinking, sleeping, etc., as well as comfort behaviour (e.g. Coutlee 1963, 1966; Delius 1969; Ficken 1962; Maxwell and Putnam 1968; Riakow 1968; Sauer and Sauer 1967; and references in McKinney 1965). This term has proved convenient as it allows a miscellany of activities which are not concerned with reproduction and not intrinsically social in nature to be treated together.

Clearly, preference for this and other alternative terms depends on the level of classification of behaviour most suited to the task at hand. The terms are not rigorously defined; rather, their utility rests on the general indication they give as to the part of the behavioural repertoire being discussed. No implication is intended that activities subsumed under the heading comfort behaviour necessarily share any motivational factors.

1.3 ORGANISATION OF THE THESIS

The next two chapters are devoted, respectively, to a general consideration of the place of comfort behaviour in ethology and to a review of research and current views concerning the immediate causation of comfort behaviour. In chapter 4 the comfort behaviour repertoire of the mallard will be described, paying special attention to movements which will be treated as dependent variables in a series of experiments, to be described in chapter 5, on the effects of peripheral stimulation on these movements. The results of these experiments will be described in chapter 6 and the sequential organisation of the observed behaviour in chapter 7. The final chapter will comprise an overall discussion of the findings and a consideration of problems yet to be tackled.

CHAPTER TWO

HISTORICAL PERSPECTIVE -- COMFORT BEHAVIOUR IN ETHOLOGY

2.1 INTRODUCTION

The traditional concern of ethology with comfort behaviour has been focused around three problems:

- 1) the phenomenon of so-called "displacement activities";
- 2) the closely allied topic of the origin and evolution of displays from non-display behaviour;
- 3) the use of comfort movements as taxonomic characters.

Other than in these contexts comfort behaviour has been ignored except for brief mention in some ethograms and scattered anecdotal accounts of the more curious activities, with an emphasis on anting, sunning, dusting and the more unusual forms of bathing. Goodwin (1956), Nice (1943, 1962) and Simmons (1964) have drawn much of this information together.

2.2 COMFORT BEHAVIOUR AND "DISPLACEMENT ACTIVITIES"

In the earlier literature on bird behaviour there are frequent accounts of birds performing certain comfort movements in situations when this behaviour seemed irrelevant to the immediate needs of the bird. Usually, these situations were such that the bird seemed to be excited and/or in a state of motivational conflict, especially if it seemed to have been thwarted in some way. Reviewing the material Tinbergen (1952) mentioned accounts of starlings, cranes and snow buntings preening their wings during fighting; ducks preening during courtship; pigeons, avocets and shelldrakes preening their wings before copulation; cormorants ruffling and shaking their plumage after disturbance; cormorants, ducks and gulls bathing after disturbance; and birds of paradise bill-wiping during display. Many similar accounts are to be found elsewhere in the literature.

Other activities too were thought to occur out of context in a similar way. Tinbergen's (1952) account lists the categories foraging movements, nest building movements, incubation and sleep as well as comfort movements.

These apparently out of context activities were called, in English, "displacement activities". This term was coined with a specific causal explanation in mind, which has now been superseded. However the label has remained useful although it is recognised that displacement activities may not be a unitary phenomenon and that there are considerable difficulties in establishing the irrelevance of an activity at a particular time (McFarland 1966). Even so, some authors prefer the term "irrelevant behaviour" to "displacement activities".

In birds, comfort movements attracted more attention than other activities when attempts were made to study the phenomenon of displacement activities in more detail. Other apparently irrelevant activities subjected to scrutiny included nest building (e.g. Beer 1961) and feeding movements (e.g. Feekes 1972, McFarland 1965), but these studies were rather outweighed by the well-known investigations of Andrew (1956 a,b), Morris (1956), van Iersel and Bol (1958) and Rowell (1961) on comfort behaviour. This emphasis is illustrated by Zeigler's (1964) review of the motivational aspects of displacement activities in which the discussion is largely in terms of comfort movements.

Undoubtedly, this concentration on comfort behaviour has been mainly due to the relative ease with which it can be observed as an apparently irrelevant activity of birds, especially in the laboratory. A contributory factor may have been the occurrence of various forms of grooming in seemingly similar circumstances in many other animals, especially arthropods and mammals. In man it has been suggested that

nail-biting and head scratching in stressful situations are directly comparable to displacement grooming and preening in other animals.

2.3 COMFORT BEHAVIOUR AND DISPLAYS

Tinbergen (1952) pointed out that some displacement activities seemed to function as "social releasers", and that those which did so often differed markedly in form from the same movements performed in the "normal" context. In contrast, those displacement activities which were thought not to affect the behaviour of other members of the species differed rather less from the normal form. This kind of observation led to the idea that the modified displacement activities had undergone evolutionary changes to fulfil their communicatory role more effectively; they were said to have become "ritualised".

The concept of ritualisation was especially attractive because it was already apparent that closely related species often utilised the same basic movement in a communicatory role, although the nature and degree of modification might differ among species. There were already a number of comparative studies of displays and these yielded a picture more detailed than was possible if non-display movements were utilised, and more closely analogous to the comparative approach of classical zoology to morphology. Lorenz's (1941) paper on duck displays is a classic example of such an approach.

Considerable attention has been paid to the evolutionary changes inherent in the process of ritualisation. Changes in the form of the movement seem to have been toward a more stereotyped and conspicuous performance, as would be expected if a more effective signal function was being evolved. There must also have been changes in the causal mechanisms underlying many such movements, a process known as

"emancipation" (Blest 1961, Morris 1957).

Tinbergen (1952) did not think that a communicatory role necessarily implied ritualisation, but thought that displacement activities in some threat situations differed from the normal form of the behaviour by the superimposition of other elements rather than by evolutionary change. Neither was it considered that all displays originated as displacement activities. For example, Moynihan (1955) suggested that display-preening in the social display of ducks may have evolved from preening in response to disarrangement of the plumage which must occur in that context.

2.4 COMFORT MOVEMENTS AS TAXONOMIC CHARACTERS

The observations of Heinroth (1930) on the phylogenetic distribution of techniques of scratching the head with the hind limb and of yawning, helped establish the idea that behaviour could be studied comparatively and led to an interest in the possible use of head scratching in particular, and comfort movements in general, as taxonomic characters. Birds scratch in one of two ways (Simmons 1961), either by lowering the wing and bringing the foot to the head over the shoulder ("indirect" or "over-the-wing" scratching) or by bringing the foot directly up to the head ("direct" or "under-the-wing" scratching). There is considerable consistency within families and lower taxa in the method used to scratch. The direct scratching of oystercatchers (Haematopidae), avocets and stilts (Recurvirostridae) supports other evidence (Simmons 1964) that they be more closely related to the true plovers (Charadriidae) than to the sandpipers (Scolopacidae). However, some families and lower taxa contain both direct and indirect scratching species, which may point to erroneous classification. This has been suggested for the babblers (Timaliidae) and new world warblers (Parulidae) by Simmons (1961) and for the parrot sub-families Loriinae and Psittacinae by Brereton and

Immelmann (1962).

The use of a variety of comfort movements in taxonomy is particularly well exemplified by Simmons' (1963) work on the babblers, a difficult group of passerines to classify. The babblers are usually classified close to or within the thrush-warbler-flycatcher assemblage Muscipcapidae. This is contrary to what might be expected from the fact that the majority of Timalid genera scratch directly whereas the others do so indirectly. Furthermore, unlike thrushes and their allies, babblers allopreen. Moreover, they employ very unusual techniques of bathing and oiling the head: instead of transferring preen-oil from the bill to the head by scratching like thrushes, babblers rub both bill and head against a wing; and whereas thrushes bathe by standing in shallow water, babblers hop in and out in a characteristic way. Simmons (1963) pointed out that these characters do not suggest a very close affinity with the thrush assemblage and also noted that the comfort behaviour of the wren-tit Chamaea fasciata, which is often placed in a family on its own, fully supports its inclusion with the Timaliidae.

Such uses of comfort behaviour as taxonomic characters have encouraged examination of the systematic distribution of other comfort movements. For instance, Clark (1970) undertook a survey of bill wiping explicitly to discover whether that activity could be taxonomically useful. Lists of taxa in which other comfort movements have been observed have also been compiled, though not necessarily to assess their taxonomic relevance, e.g. Whitaker (1957) and Simmons (1966) for anting, and Kennedy (1969) for sunning. Information collected on the systematic distribution of certain comfort movements raises tantalising questions concerning function (e.g. why do very few species both ant and dust) and evolutionary derivation (e.g. in sparrows Passer dusting resembles bathing, in pigeons (Columbidae) sunning resembles rain bathing and in various species

passive anting resembles sunning) (Simmons 1964).

The very well known paper by Lorenz (1941) on the displays of various ducks contains many ideas relevant to the three themes of displacement activity, the origins of displays and behavioural taxonomy. More recently, McKinney's (1965) paper on the comfort behaviour of the Anatidae was exceptional in its detailed coverage of so many discrete movements discussed with reference to a wide range of species, and also in that it provided something of a synthesis of these three approaches to comfort behaviour.

CHAPTER THREE

THE CAUSATION OF COMFORT BEHAVIOUR

3.1 INTRODUCTION

As Zeigler (1964) emphasised in his review of the subject, the phenomenon of displacement activity has deep implications for motivational theory in general and so, not surprisingly, it has been the subject of much research. We have already seen that a large proportion of the studies on displacement activities has examined comfort behaviour. This work forms the core of what has been empirically discovered about the causation of comfort movements. The rationale of using information so gained rests on the assumption that there is much in common in the causation of comfort behaviour in "normal" and "displacement" situations (see below).

A few authors, notably Andrew (1956 a,b) and McKinney (1965) have explicitly been concerned to know more of the causation of "normal" and "displacement" comfort behaviour so as to better understand the ritualisation of such movements into displays. To fully understand emancipation - the evolutionary change in causation presumed to accompany ritualisation of a movement - it is desirable to understand the causation of both pre- and post-ritualisation versions of the movement. Unfortunately, the emphasis has been very much on displacement activities as the immediate precursors of displays, and the possibility of the non-displacement form of a movement evolving directly into a display without the intervening stage of its occurring as a displacement activity, has been largely neglected.

3.2 BACKGROUND TO RESEARCH ON COMFORT BEHAVIOUR AS DISPLACEMENT ACTIVITY

A characteristic feature of displacement activity is its apparent irrelevance. In general terms this implies that stimuli which normally elicit the activity were absent or ineffective when it was performed as an irrelevant activity. The original formulation of the mechanism

producing displacement activities (Tinbergen 1952) was that one motor system was blocked in some way and its accumulating motivational energy "sparked over" or was "displaced" on to another motor system through which it discharged. Following Kortlandt (1940), when an activity resulted from the discharge of energy from another motivational system it was said to be "allochthonously motivated". In contrast, an activity resulting from the expression of its own drive was said to be "autochthonously motivated".

However, it was already apparent to Tinbergen (1952) that external stimuli played a role in determining which movements would be performed as displacement activities. Thus the distinction between autochthonous and allochthonous motivation was ill-founded. From this followed the formulation of the "disinhibition hypothesis": an activity was thought to be expressed following the removal of inhibitory influences from other types of behaviour which were incompatible with the first. In conflict situations these other activities were thought to inhibit one another, so disinhibiting the first activity.

In contrast to the original autochthonous/allochthonous distinction, the disinhibition hypothesis and most other later theories of displacement activity clearly imply that at least some of the causal factors for comfort behaviour in displacement situations are those which also operate in other situations. Hence the inclusion of evidence from research on displacement activities in a consideration of the causation of comfort behaviour in general, especially as there has been little research on comfort behaviour not from this perspective.

Three studies in particular, namely those by Andrew (1956 a,b), Rowell (1961) and ^{vem} Iersel and Bol (1958), are noteworthy as contributing to the development and expansion of the disinhibition hypothesis

specifically via analyses of the causation of comfort behaviour in birds.

In laboratory studies, Andrew and Rowell tended to emphasise the role of peripheral stimuli whereas ^{van}Iersel and Bol, in a field study, dwelt largely on endogenous factors. A discussion of the effects of ambient temperature, especially upon feather posture, featured prominently in Andrew's contribution. Contemporaneously, Morris (1956) was working along similar lines, which subsequently has been taken a little further by McFarland and Baher (1968). Delius (1970) has focused on the often-observed association between comfort behaviour and sleep and has incorporated this into a rather novel theoretical treatment of displacement activities. McKinney's (1965) work stands out as rather different in outlook from these other workers, being a broad, qualitative, comparative approach to comfort behaviour in "normal", "displacement" and "display" situations among the anatidae.

3.3 ANDREW'S HYPOTHESIS

Andrew (1956a) was the first to explicitly suggest that certain irrelevant activities might be caused by the same influences which operate in normal circumstances. He pointed to the occurrence of thermoregulatory-like responses in apparent "displacement situations" and suggested that these could be secondary effects brought about by changes in body temperature due to autonomic activity during conflict etc.. In a subsequent paper (Andrew 1956b) he extended these ideas to other forms of comfort behaviour, suggesting that the peripheral stimuli which elicit most comfort movements are continuously present but the movements themselves are usually suppressed by other types of behaviour. Comfort movements usually occur when other tendencies are weak, but may also appear, by disinhibition, when stronger tendencies suppress one another in moments of transition between two activities or when tendencies

to perform incompatible activities are in conflict.

Andrew (1956b) briefly described some experiments with buntings (Emberiza spp) which illustrated the kinds of peripheral stimulation that facilitated these activities. Raising the ambient temperature resulted in panting, gaping, bill-licking, feather-sleeking, wing-raising and sunning while cooling was observed to result in feather erection and shivering. When the birds were sprayed with water they engaged in bill-wiping, feather-settling, preening and scratching etc. Bill-wiping seemed to be facilitated also by unpleasant tastes or foreign bodies on the bill. Derangement of the body feathers was observed to provoke preening. Yawning and gaping were thought to occur in response to irritation of the respiratory passages, and stretching in response to proprioceptive stimuli from cramped or inactive muscles.

Although his emphasis was very much on causation by peripheral stimuli, Andrew did not entirely neglect possible "central" causation. He suggested that stretching and yawning might be temporally associated by virtue of their having (central) causal factors in common. Endogenous factors might also explain the association of feather-raising and bill-wiping and the persistence of the tendency to bathe. On the other hand, Andrew pointed out that the temporal association of sleep, stretching and other comfort movements may result from the sharing of permissive factors - if they were all easily suppressed by other tendencies then they would tend to occur together when those tendencies were weak.

3.4 COMFORT BEHAVIOUR, AMBIENT TEMPERATURE AND THERMOREGULATORY RESPONSES

Andrew's (1956b) point about the effects of ambient temperature has received further attention from other authors. Morris (1956) reported that, as well as fluffing their feathers in the cold and sleeking them in

heat, birds exhibited a very high degree of feather erection and also sunning when subjected to intense heat from photographic lamps. Following Moore (1945) Morris interpreted this as a functional cooling response, contending that the air spaces in the plumage opened to the outside air, so reducing insulation. However, McFarland and Baher (1968) failed to find feather raising in doves at high ambient temperatures in normal illumination, but extreme feather erection was exhibited at high illumination in normal temperatures. The illumination rather than the ambient temperature was probably the effective stimulus for extreme feather erection.

McFarland and Baher also provide evidence which goes against Andrew's (1956a) view that feather sleeking in frightened birds and feather erection in aggressive ones is due to thermoregulatory responses to the effects of autonomic activity. In birds subjected to changes in ambient temperature, feather posture changes were more or less uniform ~~over various~~ areas of the body surface, unlike the distribution of feather posture changes when the birds were made aggressive.

3.5 COMFORT BEHAVIOUR AND SLEEP

Andrew (1956b) briefly mentioned the association between comfort behaviour and sleep, which he thought of as being due to both types of activity being permitted by the absence of stronger tendencies. Delius (1967, 1970) has gone further than this and suggested that it is advantageous to the animal for there to be a more direct causal connection between sleep and comfort behaviour and that comfort behaviour, in certain situations, is activated by a sleep or "de-arousal" control system. Comfort behaviour performed by active awake animals in normal circumstances is assumed to be due to strong peripheral stimulation.

In contrast, displacement comfort behaviour, like comfort behaviour associated with sleep or drowsiness, is due to the activation of the de-arousal system. Delius conceives arousal as being related to the rate of information processing by the animal. In displacement situations, he suggests that the optimum rate, i.e. optimum arousal, is exceeded and so a homeostatic de-arousal system is activated. Displacement comfort movements are thought to occur as an epiphenomenon of this process. Other drowsiness-associated comfort behaviour is assumed to be due to the normal activation of the de-arousal system, e.g. preparation for sleep.

In support of this hypothesis Delius discusses his own work with gulls, and that of others on a variety of bird and mammal species, that shows that signs of drowsiness and the activities commonly associated with this, including various comfort movements, can be elicited by electrical stimulation of the brain and by drugs, and that these activities are just those which occur as species-typical displacement activities. Furthermore, performance of comfort movements is often accompanied by electrophysiological signs of de-arousal.

While accepting that appropriate peripheral stimulation can enhance displacement activities (and also, presumably, the same activities in the normal drowsy state) Delius makes the very important point that there is no evidence to support the prediction, implicit in the disinhibition hypothesis, that non-typical displacement activities can be made to occur by manipulating the animal's motivational state. Thus some doubt must remain about the assumption, made in the various versions of the disinhibition hypothesis, that the reason why a small number of movements predominate as species-typical displacement activities is that these activities have a more or less continuous low level of activation and

in this respect are unlike other types of behaviour. With this doubt about the "passive" disinhibition model, some kind of "active" mechanism as suggested by Delius (and by others for fish and mammals, e.g. Wilz (1970), Fentress (1968)) must be entertained, at least as a possibility.

3.6 VAN IERSEL AND BOL'S MODEL

In their study of displacement preening etc. in terns (Sterna Spp) ^{van} Iersel and Bol (1958) adopted a position somewhat similar to Andrew's and extended the disinhibition idea by suggesting that the occurrence of displacement activities resulted from some form of blocking of other tendencies which were otherwise strong enough to over-ride and rule out the performance of comfort movements. Again, like Andrew, they recognised the need to understand the causation of comfort behaviour in the normal context, i.e. in the terminology then current, its autochthonous occurrence. ^{van} Iersel and Bol's position differed from that of Andrew primarily in that they placed far more emphasis on the endogenous causation of comfort behaviour.

As an example of autochthonous preening, ^{van} Iersel and Bol studied the preening of birds after bathing, paying special attention to the distribution of preening directed at different areas of the body surface and how this and the frequency of other comfort movements changed as the preening bout progressed. The basic finding was that the relative frequencies of different movements peaked at different stages through the bout.

To explain this temporal patterning ^{van} Iersel and Bol proposed a model based on the postulate of a fluctuating "preening drive" which was thought to activate the various movements at different thresholds. This preening drive was thought to be low at the beginning of the bout,

to increase rapidly to a maximum and then to decline more gradually. Movements dominating the early and later phases of the preening bout were thought to have respectively low and high thresholds.

In support of their drive-threshold model^{Van}/Iersel and Bol drew on three other lines of evidence: the form of the movements, the frequency of the movements and the distribution of bout lengths. The first of these is based on the assumption of a correlation between the complexity of a movement and the drive level at the time. Movements occurring early in the bout were reported to be very often rapid and incomplete, thus supporting the idea of an initially low preening drive. Moreover, the purported high threshold movements (shaking, preening the inside of the wing, the tail and the pinions, and head-rubbing) were more complex in form than the low threshold ones (head-shaking, breast-preening and shoulder-preening). The second point is based on the assumption that the rate of performance of all the various preening movements considered collectively (number of movements per minute) co-varied with drive level. This rate of performance peaked early in the preening bout and then progressively tailed off. Van Iersel and Bol showed that the number of purportedly high threshold movements, as a proportion of all movements, was correlated with the number of all movements in the same minute. Thirdly, longer preening bouts showed a drop in movement frequency and a peak of purported low threshold movements around the fourth minute - a time when shorter bouts tended to terminate; just what might be expected from a marked drop in the level of the preening drive at around that point in the bout.

Although^{Van}/Iersel and Bol claimed to use the term drive in a wide sense to include appropriate sensory input, they explicitly stated that they regard the preening drive as "mainly the complex of internal factors". Further they claimed that "the large number of observations

(under similar circumstances) exclude the possibility that the observed variations in frequency and intensity of preening are (only) due to variations in the strength of external stimulation" (p5, parentheses as in original). ^{Von} Iersel and Bol did present some data on the influence of rain on comfort behaviour: rain seems to facilitate various comfort movements, mainly head-shaking, during brooding. In accounting for this the emphasis was on the effect of rain as "direct stimulation of the preening system" (p75) rather than a more specific effect of rain on head-shaking. Head-shakes were thought to predominate in such circumstances because they are low threshold movements, even though it was recognised that this posed quite a lot of difficulties for the model and does not fit in with the increase in the frequency of comfort movements brought about by rain.

3.7 ROWELL'S MODEL

Rowell (1961) quite explicitly set out to show that displacement "grooming" in the chaffinch could be accounted for "solely in terms of variation of definable factors, especially peripheral stimulation, without postulating avoidable intervening variables such as grooming drive" (Rowell 1961, p39). His position was that preening in birds in approach-avoidance conflicts could be understood by reference to three factors: 1, adequate external stimulation; 2, the conflicting tendencies being in a state of equilibrium; 3, the equilibrium state to last for a sufficient length of time.

Rowell produced some intriguing evidence to support this view. He showed that wet plumage increased the probability of "grooming" (mainly body-shaking) in both "normal" and conflict situations. Moreover, he showed that a sticky bill increased the frequency of bill-wiping with

little effect on other comfort movements. Secondly, reasoning that approach and avoidance tendencies were more likely to reach equilibrium in pauses with a change in direction between approach and avoidance than in pauses with no such change, Rowell showed that grooming was more likely in the former type of pause even when the extra length of "turning" pauses was taken into account. Thirdly, Rowell showed a convincing positive correlation between length of pause and the probability that grooming would occur during a pause, even allowing for the possibility that grooming caused a pause to be longer, which in fact did not appear to be the case.

In accord with his position Rowell appended to his paper a model which could explain sequential changes in the relative frequency of different comfort movements, which both he and ^{Van}Iersel and Bol observed, without postulating a variable preening drive. This model retained the postulate of threshold differences for the different movements and emphasised the notion that grooming is a response to peripheral stimulation. Two other, intuitively reasonable, assumptions were also required: that grooming decreases the stimuli producing it and that activation of different responses is graded according to the extent to which stimulation exceeded the various response thresholds.

Although such a model would account for the observed sequential changes, Rowell expressed his dissatisfaction with such explanations, especially as different comfort movements might be activated by qualitatively different forms of input, a plausible explanation which brings into question the whole rationale of arranging such stimuli on a single threshold scale, which is, after all, tantamount to postulating a single variable such as a preening drive, albeit primarily exogenously activated - something which Rowell wanted to avoid.

3.8 MCKINNEY'S WORK ON THE COMFORT BEHAVIOUR OF THE ANATIDAE

McKinney (1965) was not primarily interested in problems of the causation of behaviour; rather he was concerned to develop a broad understanding of comfort behaviour in wildfowl, especially its "primary" functions of caring for the body surface, in order to provide a basis for deductions about comfort movements in "secondary situations" - when they might be irrelevant or have some signal function. Nevertheless, his broad, comparative, observational material provides a wealth of suggestions regarding the causation of comfort movements and, in addition, he devotes one section to the explicit discussion of causation.

The comfort movements which seem to have a signal function McKinney believes to be controlled by conflicts between attack, escape and sexual tendencies - the classical theory of the motivation of displays (Hinde 1970, Marler and Hamilton, 1966). In circumstances when the apparently irrelevant performance of comfort behaviour probably has no signal function, McKinney clearly looks first for possible explanation in terms of exogenous stimuli. He considers quite plausible the idea developed by Andrew (1956a) that autonomic responses could generate appropriate peripheral stimuli. He also gives considerable credence to the type of mechanism suggested to Lind (1959) where the immediately preceding activity could generate additional peripheral stimuli just before the occurrence of comfort behaviour, such as occurs soon after alighting, disturbances, hostile encounters or copulation - just when one might expect the plumage to be wetted and/or deranged. (On the other hand, Nilsson (1965) studied the behaviour of goldeneye (Bucephala clangula) in just these situations and chose to interpret them in relation to Iersel and Bol's model, but neither he nor Lind nor McKinney carried out any critical quantitative or experimental work which could distinguish between the possibilities.)

With comfort behaviour in clearly "basic" situations too, McKinney's inclination is toward suspecting exogenous stimuli arising from the situations in which a bird finds itself and, especially, from what it has just been doing. Dirt getting on to the bill or plumage as a consequence of feeding activities releasing bathing and stimuli from bathing releasing oiling are examples of the kind of process that McKinney suspects may operate. He criticises ^{Van}Iersel and Bol's model on the basis of their neglect of the possible significance of peripheral stimuli, especially water and preen-oil on the plumage. Water, dirt, loose feathers, pieces of weed, and irritation from ectoparasites, and the strength and position of these stimuli on the body are all cited as likely causal factors for a variety of comfort movements. Nonetheless, McKinney does hold that endogenous factors play a role, especially in diurnal patterns of activity, and in short term sequences of movements. In general, he clearly wishes to emphasise the complexities involved and to hold an open mind about the principles of causation of various movements in many circumstances.

3.9 THE PRESENT INVESTIGATION

The preceding discussion illustrates how two inter-related issues thread their way through the various differences in agreement and emphasis. The first concerns the extent to which factors controlling comfort behaviour are peripheral in origin: the problem of exogenous versus endogenous control. The most important peripheral input is assumed to be cutaneous although tactile (from the bill) and visual inputs are also likely to play a role. The second question concerns the degree to which causal factors are shared by different activities and the degree to which different activities are evoked by qualitatively different factors (the problem of general versus specific control).

This applies to causal factors which comfort movements share with other activities as well as causal factors shared between different comfort movements.

These two questions could be tackled in a number of ways. It would be very informative to know something of the characteristics of comfort behaviour when cutaneous input was held constant or eliminated, an approach which would probably require surgical intervention. It is also important that we should know more of the causal relationships with other types of behaviour. Although highly relevant these questions are beyond the scope of the present enquiry. There is still much to be learned from further exploration of the effects of changing peripheral stimulation on comfort behaviour.

The obvious next step in this direction is to go beyond observing the effects of rather haphazard changes in the stimulus condition of the body surface following rain or experimental spraying, as was done by Andrew (1956b), Rowell (1961), ^{Van} Iersel and Bol (1958) and Delius (1969). What is required is systematic manipulation of cutaneous input while monitoring as wide a range as possible of different comfort movements. Such an approach should tell us something of the degree to which different movements are elicited by qualitatively different (cutaneous) stimuli. This is the course taken in the present investigation. The comfort movements involved are described and defined in the next chapter and the forms of experimental treatments and their effects in subsequent chapters.

CHAPTER FOUR

UNITS OF COMFORT BEHAVIOUR IN THE MALLARD - TERMINOLOGY
AND DESCRIPTION

4.1 GENERAL SCHEME

An effort was made to follow McKinney's terminology for the comfort movements of the Anatidae. However, in many cases McKinney's system was unsatisfactory and had to be modified. In particular, McKinney separated preening movements performed during bathing, calling them "washing", and preening movements performed while oil from the uropygial gland is being spread on the plumage, which he called "oiling-preening", from preening in other contexts, even though very similar if not identical movements are involved. In the present study, the movement of actually taking oil from the uropygial gland is recognised as a distinct movement, and most of the other movements which McKinney included in "oiling-preening", "washing" and "nibbling-preening" are treated as either rubbing or preening and subdivided according to the area of the plumage toward which they are directed.

There are other departures too from McKinney's qualitative division of comfort behaviour into units. These will be discussed together with the descriptions of the movements which follow. For convenience of description the various comfort movements are categorised as shaking movements, stretching movements, preening movements and bathing movements. This classification too differs slightly from McKinney's.

Because of limitations in recording etc., some movements received more attention than others. At a descriptive level a lot of attention was paid to body-shakes, partly because of their similarity to the ritualised "introductory-shake". In the experiments emphasis was on shaking, preening and associated movements as these were thought most likely to be affected by the treatments used. No attempt was made to record stretching and yawning movements and some comfort movements, which normally occur at a rather low frequency, did not occur during

the experiments. Nevertheless, for the sake of completeness, as much as possible of the complete repertoire of comfort behaviour of the Mallard will be described.

For quantitative purposes the behavioural units recorded in the experiments were treated as point events which could be counted to yield a frequency measure. The boundary of what constitutes one unit of each of these movements is specified in the following account. The exception to the point event scoring system was the tail-wag which was recorded only in experiments 9 and 10; here tail-wags were treated quantitatively as cumulative durations.

There were a few changes in the units of behaviour recorded as the series of experiments progressed. For instance, in the early experiments dip-shakes were not distinguished from bill-dips and head-shakes, and preening and rubbing of the flanks were not separated. These points are explicated below.

4.2 SHAKING MOVEMENTS

4.2.1 Body-shakes. These are movements involving a general shaking and feather ruffling over the greater part of the body, progressing from posterior to anterior. The movement is initiated by a lateral movement of the tail, of increasing intensity, i.e. the frequency and amplitude of the movement and the extent to which the tail is fanned, all increase. Next, the feathers on the trunk are erected and the wings, especially the secondaries may be shaken in their folded position, often being shaken out of the "pockets" in the flank feathers. Finally, at the climax of the body-shake, the head and neck are raised and rotated in a manner similar to but distinguishable from the head-flick. At this point the tail is typically in an elevated position. One can see

from high speed film that when the vigorous wing movement is absent the apparent shaking motion of the trunk and the slight movement of the wings is purely a secondary effect resulting from the shaking of the tail as a preliminary to the body-shake, from the neck shaking at its climax and, in a body-shake performed whilst afloat, from the paddling action of the feet. During the shaking of the neck, water droplets can be seen to be thrown from the breast as well as from the head, and it is the force from this neck-shaking component which may make the feet slide apart when a bird body-shakes while standing on a slippery surface.

In the experiments body-shakes were recorded as single units disregarding their components. Body-shakes were given the names standing-shake or swimming-shake depending whether they were performed while standing or while afloat. For completeness one might add the term flying-shake for a body-shake performed during flight, but such movements are uncommon and were not observed during the experiments. The major difference in form between standing-shakes and swimming-shakes is the presence of alternate paddling action of the feet in the latter, which raises the body out of the water. The difference is common to many actions of ducks which may be performed either in or out of the water.

It should be noted that McKinney restricts his term "body-shake" to standing-shakes other than what he called "wing-shakes". Here it is used to encompass several combinations of a number of components which are clearly recognisable as a group of closely related activities. It is useful to have a general term for these movements - McKinney used "shake" or "shaking" when it was clear from the context whether the movement was performed on land or on water. However McKinney also usefully employed "shaking movements" as it is used here, as a category to include wing-flaps, head-shakes, head-flicks, foot-shakes, tail-wags

FIGURE 4A Standing-shake.

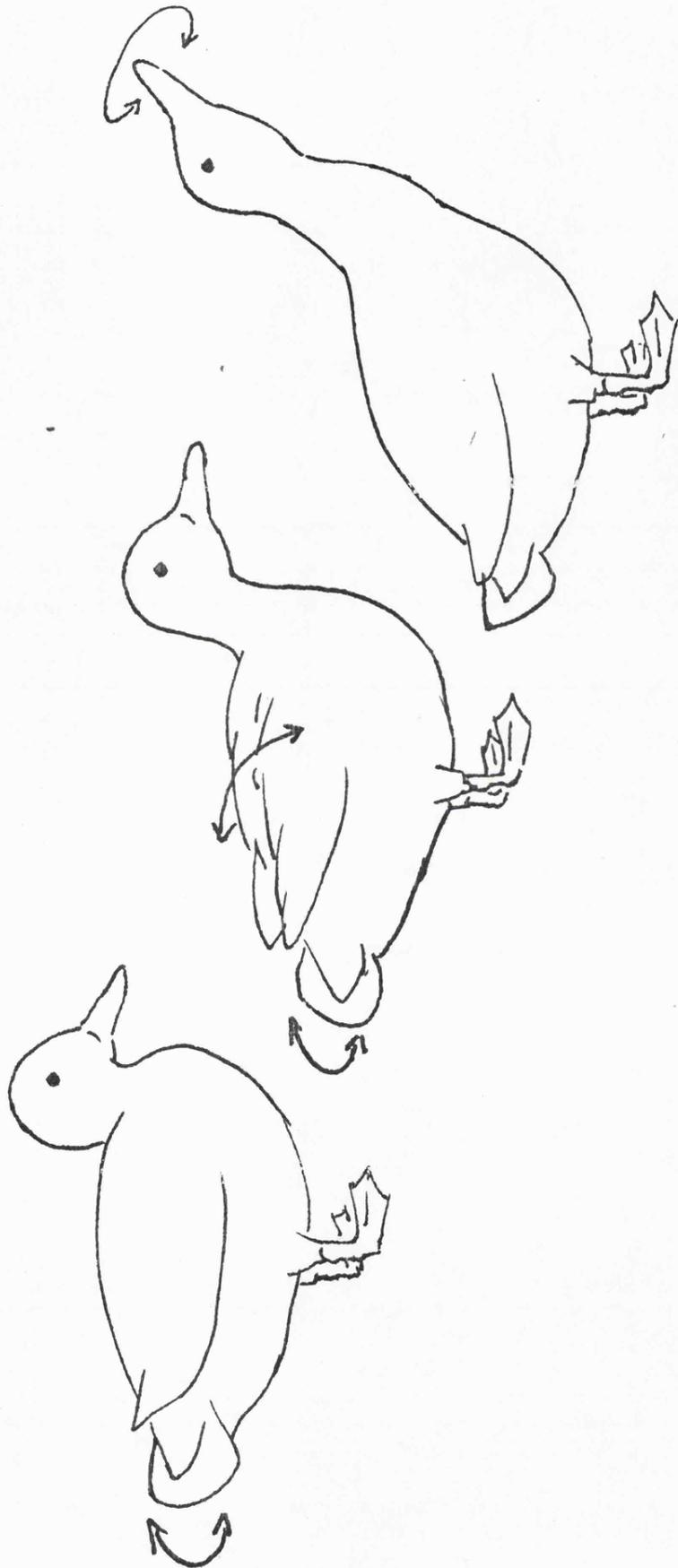
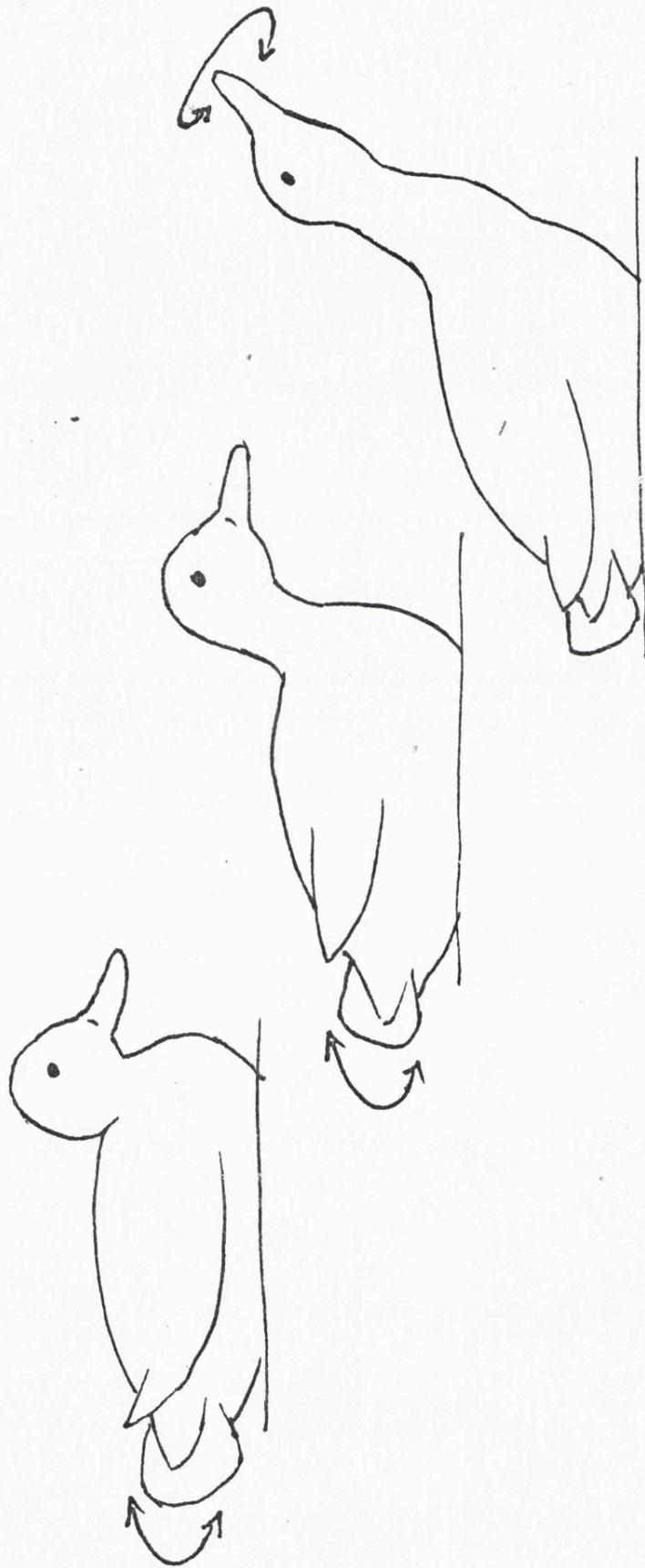


FIGURE 4B Swimming-shake.



etc. as well as body-shakes. I do not feel that I can consistently separate what McKinney called "wing-shakes" from what he called "body-shakes" so I have lumped these together as "standing-shakes" and used "body-shakes" as a more general term.

The characteristics that McKinney used to distinguish "wing-shakes" from other standing-shakes were that in the former the preliminary tail movement might be absent, there is no head movement and the wings (mainly the secondaries) are shaken more vigorously than in other types of standing-shake. This distinction is a matter of the occurrence or non-occurrence of components of body-shakes. Vigorous wing movements, as McKinney described, occur frequently in standing-shakes, together with neck and head shaking. This combination is especially characteristic of the initial stages of drying, i.e. when the duck is at its wettest. This type of standing-shake predominated in films of birds whose undersides (belly and breast) had been experimentally wetted although their wings were apparently no wetter than is usual in a duck that has recently bathed.

McKinney noted that intermediates between his "body-shake" and "wing-shake" did occur, but he interpreted them as "wing-shakes" followed closely by a head-flick, or as a "body-shake" (in his usage) with the head movement absent and with low intensity wing movements. He considered that the occurrence of his "wing-shakes" in the very definite context of oiling-preening indicated that it should be distinguished. I agree that the particular combination of movements described by him as a "wing-shake" is indeed characteristic of oiling-preening but it is not confined to that context. Moreover other combinations of the components of body-shakes are typical of other contexts (although there is considerable overlap) so there is little point in selecting just the "wing-shake" combination as a special case.

Vigorous wing movements occur only very rarely, if at all, in swimming-shakes, even in ducks oiling while afloat or those which have been experimentally wetted. McKinney too noted that he had never seen a swimming bird "wing-shake". In contrast swimming-shakes with the head and neck movement reduced or absent are not uncommon, and are especially characteristic of birds which for one reason or another perform swimming-shakes more frequently than normal. McKinney observed ducks which had lost the waterproofing of the breast feathers, repeatedly performing swimming-shakes. This is the type of situation in which the abbreviated swimming-shakes are given. Such movements are typical of ducks suffering from "wet-feather" or in the early stages of moult, when their water repellency is impaired. Experimental wetting (see next chapter) does not produce these abbreviated swimming-shakes.

4.2.2 Head-flick. This is a movement of the head and neck which gives the global impression of being a "rotary-head-shake" or a "neck-stretching-and-shaking". Analysed in more detail with the aid of high speed film the movement is seen to be the combined effect of two elements. The neck is extended forward and upward and the neck is raised from the position of normal carriage with the bill pointing downward, to a position where the bill is pointing upward in line with the neck. Superimposed upon this movement of the head in the vertical anterior-posterior plane, is a rotation of the head and neck. In the initial stages of the head-flick the bill is pointing downward and so moves laterally in a manner similar, if not identical, to a head-shake; whereas at the highest position of the head, being in line with the neck, it rotates around its axis. In fact, because the two elements are superimposed, the bill tip moves forward and upward in a zig-zag action.

In some head-flicks the initial movement of the bill is much more

obvious than is normal, giving the appearance of a movement intermediate between a head-shake and a head-flick. It seems that in these cases the rotary element begins before the raising of the head so that the first movements of the bill are sideways rather than diagonally upwards and sideways. Such movements could be considered to be head-shakes very closely followed by head-flicks or as head-flicks in which the raising of the head and extension of the neck is out of phase (delayed) with respect to the rotary element.

In the experiments any movement in which the head was rotated and also raised forward and upward was recorded as a head-flick unless there was a noticeable pause in the first element before the upward movement started.

4.2.3 Head-shake. A rotary movement of the head and neck with the bill pointing downward, so that the tip of the bill moves laterally to and fro. The term is as used by McKinney except that a special form is distinguished as a dip-shake.

In the experiments this movement was recorded in units of one or more rapid lateral movements of the bill terminated by a noticeable pause.

4.2.4 Dip-shake. The bill is immersed in the water and rapidly shaken from side to side before being withdrawn, as distinct from a head-shake being performed during the last stages of withdrawal of the bill from the water, e.g. after a bill-dip. In a dip-shake the amplitude of the lateral movement of the bill is less and the bill is more deeply immersed than in a head-shake. The dip-shake is very distinctive. Like bill-dips, dip-shakes are often followed by head-shakes, a situation in which the difference between the two movements is particularly clear. A movement quite similar to a dip-shake is sometimes seen before a

FIGURE 4C Head-flick.

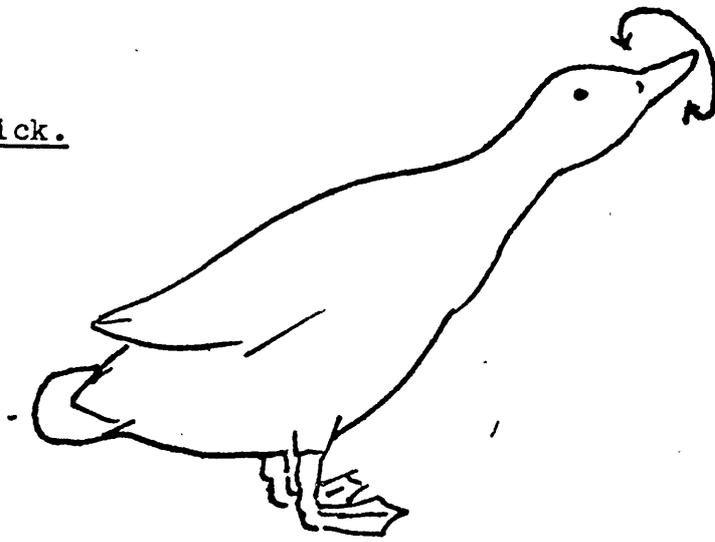


FIGURE 4D Head-shake.

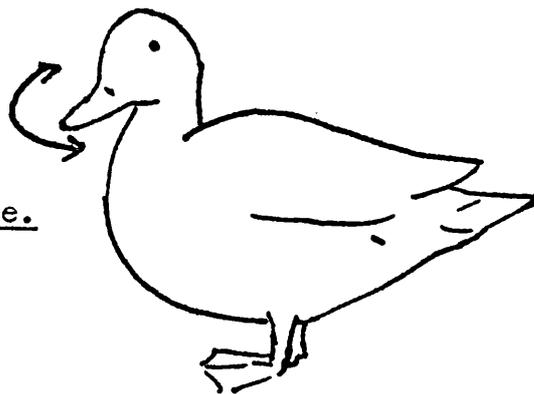
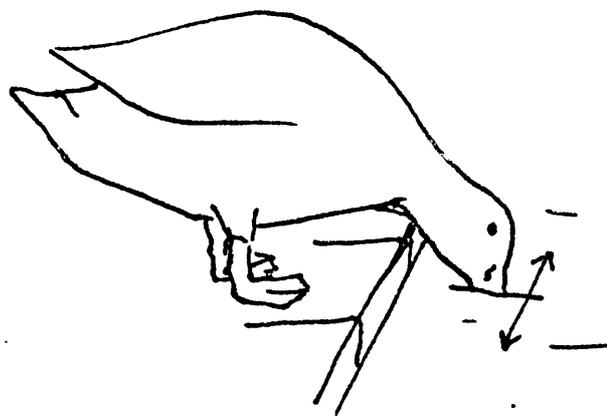


FIGURE 4E Dip-shake.



bathing bout, and is probably an incipient head-dip.

Following McKinney, in the early experiments, dip-shakes were treated as bill-dips followed by head-shakes. Thus the sequence dip-shake to head-shake was recorded as bill-dip to head-shake to head-shake. In experiments 7 and 8, dip-shakes were distinguished and recorded as single events terminated by a noticeable pause in the lateral movement of the bill.

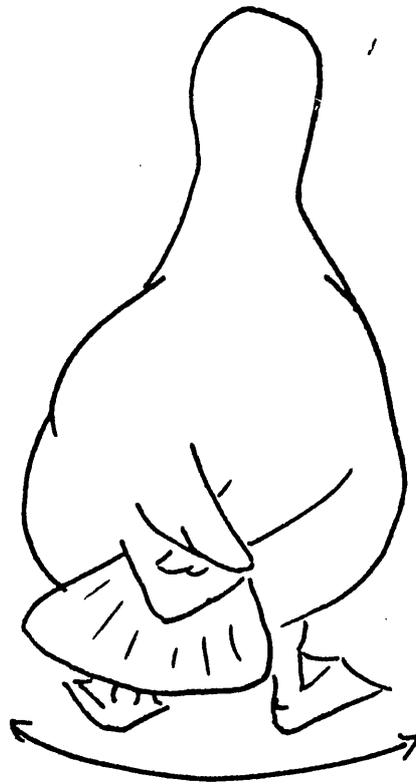
4.2.5 Bill-dip. The bill is briefly immersed in the water and immediately withdrawn without being shaken. As discussed above, they were not separated from dip-shakes in early experiments.

4.2.6 Nasal blow. This is a movement similar to the dip-shake except that air is blown out through the nostrils while the bill is submerged and being shaken. McKinney called nasal-blowing "bill-cleaning" but as this term has such strong and inaccurate functional connotations and no long tradition of usage, a change seems desirable. Although often observed during the experiments, especially after dilute detergent was thought to have trickled into the nostrils, nasal-blowing was not systematically recorded.

4.2.7 Tail-wag. The tail, which may or may not be fanned, is shaken laterally.

In the experiments it was found to be impossible to devote sufficient sustained attention to tail-wags to record them consistently as they occur concurrently with so many other activities. It was decided to record tail-wags in the two experiments involving wetting of the ventral region at the expense of collecting data on other movements. Nevertheless, because tail-wags are so ill-defined as single events, the total

FIGURE 4F Tail-wag.



time spent tail-wagging was recorded using a cumulative stop-clock. In these experiments it was noticed that some especially vigorous tail-wags were performed with the rear end of the body elevated above the water, by the adoption of a posture similar to the "down-up" display and to the position momentarily adopted after a swimming-flap, when the forebody sinks low in the water. These quite distinctive "elevated-tail-wags" were recorded as single events - a series of vigorous lateral movements of the tail terminating when the intensity of the wagging or the elevation of the rear end of the body declined markedly.

4.2.8 Wing-flaps. The wings are spread and flapped strongly, forward and backward several times, with the body in a more upright position than its normal carriage. Contrary to McKinney's description, the flapping is not quite as in flight, there being greatly reduced lift. Wing-flaps are either standing-flaps or swimming-flaps depending upon the medium in which they are performed. The difference is that swimming flaps include a paddling movement of the feet which raises the body out of the water into a near vertical position.

In the experiments wing-flaps were recorded as bouts of flapping movements of the wings terminating in a pause during which the body subsided on to the water or into the normal standing posture.

4.2.9 Foot-shake. The foot is shaken or waved at the side of the body usually before stowing it in the flank feathers. Sometimes the foot is repeatedly shaken, stowed in the flank feathers, taken out, shaken, stowed again and so on, as if to position it correctly in the stowed position. Incipient forms of head-scratching, foot-pecking and wing-and-leg-stretching are quite similar to foot-shaking. Although frequently observed, foot-shaking was not consistently recorded in the experiments.

FIGURE 4G Standing-flap.

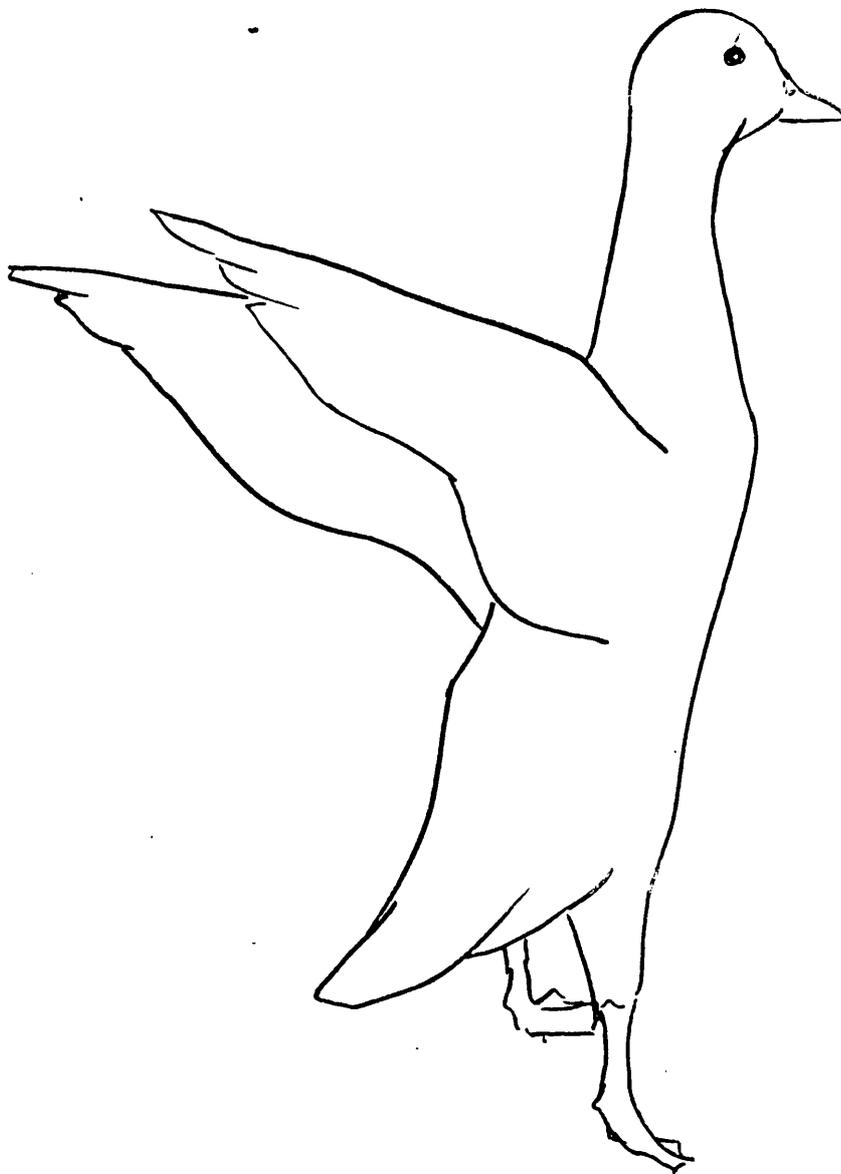
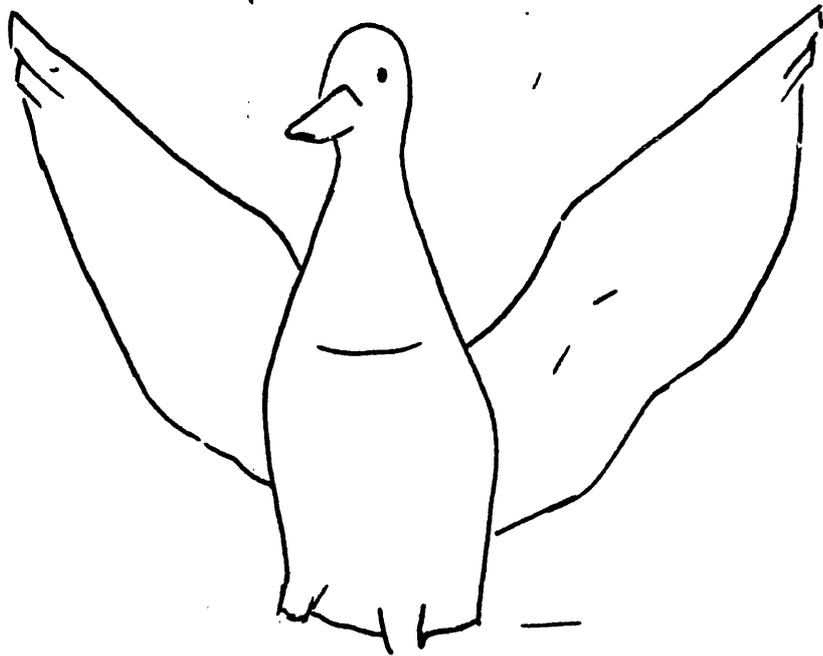


FIGURE 4H Swimming-flap.



4.2.10 Wing-twitching. Rhythmically or intermittently, the wings are lifted a little from the sides and back and the primaries fanned slightly. The movement of the wings is often slightly out of phase, i.e. there may be a "drift" between their alternate and simultaneous movement. At the same time, the retrices may be spread into a fanned position, a component which could be called tail-twitching. The lifting of the wings, fanning of the primaries and spreading of the retrices are in the form of a very rapid twitch followed by a gradual return to the normal position. At its highest intensity, i.e. when twitching is most frequent, the wings are dropped a little so that they are not crossed and the rump is exposed, as depicted by McKinney. As the intensity of the wing-twitching decreases the scapulars are crossed, and at a still lower intensity, the tips of the primaries too. Once the wings are crossed they are periodically flipped up a little and recrossed so that the one which was previously above now lies below the other. The wings may be twitched so vigorously that they leave their flank pockets, in which case they are replaced by a similar flipping movement, an action which occurs in many situations in which the wings are being resettled in their flank pockets.

The nearest thing to sunning in the Anatidae is a posture with the wings drooped at the sides leaving the back and rump exposed. This is similar to the posture during wing-twitching but wing movements are absent, and the wings may be allowed to remain outside the flank pockets. McKinney considered this "drooped wing condition" low intensity wing-twitching. The two records which Kennedy (1969) cites as sunning in the Anatidae do not refer to this posture and neither do they seem likely to be examples of sunning proper.

McKinney called wing-twitching "wing-shuffle-and-tail-fan" but he also used the term wing-shuffling to describe the movement of the wings

during head-dipping bathing. Wing-twitching is used to avoid ambiguity and to stress the nature of the movement. It was not recorded consistently in the experiments.

4.3 STRETCHING MOVEMENTS

Although these were occasionally observed, they were not recorded in any of the experiments.

4.3.1 Wing-and-leg stretch. One wing and the corresponding leg are extended backward. Occasionally, either the leg or the wing extension may be absent, and often the leg remains extended after the wing is retracted. A forward extension of the neck into a horizontal position, with the chin pressed down and the bill pointing upward slightly, sometimes accompanies the limb extension. I have once seen a female Mallard extend one (the right) leg and both wings, the left wing being extended slightly later and to a lesser extent than the right one.

4.3.2 Both-wings-up-stretch. Both the wings, folded, are raised above the back. An extension of the neck as described above usually accompanies the wing movement, much more frequently than in the wing-and-leg-stretch, and may itself be accompanied by gaping or mandibulation.

McKinney termed this movement the "both-wings-stretch". The "up" is inserted to avoid possible confusion with other stretching movements, not normally occurring in the Anatidae, which also involve the movement of both wings, e.g. the "both-wings-down-stretch" of the Rallidae and other birds (Nice 1962).

4.3.3 Yawn. The mandibles are opened briefly and closed again. McKinney called this movement a "jaw-stretch" because of doubts which

FIGURE 4J Wing-and-leg-stretch.

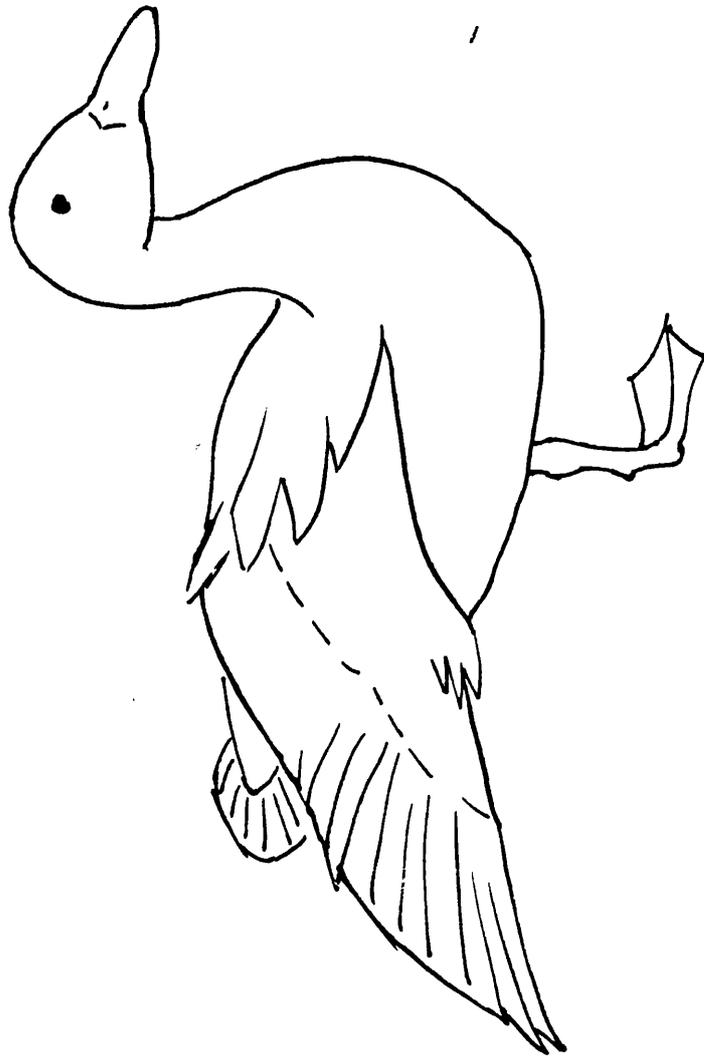


FIGURE 4K Both-wings-up-stretch.



have been expressed as to whether birds yawn like mammals. However, it is no more certain that the movement serves to stretch the jaw muscles. The differences in the respiratory apparatus of birds and mammals preclude, at that level, exact homology of their "yawning". Nonetheless, a similarity in the characteristics of inhalation and exhalation seems to be the accepted criterion (McKinney) and Sauer and Sauer (1967) have shown that in this respect avian "yawning" does exist. Simmons (1970) distinguished two movements, which he called a yawn and a jaw-stretch, in both the great crested grebe Podiceps cristatus and the brown booby Sula leucogaster. The Anatidae too have more than one kind of movement involving the opening of the mandibles. I feel sure that one such movement, usually performed when the bird is in a relaxed position with its head sunk in shoulders as depicted in McKinney's photograph, merits the term yawn. In cold weather condensation may be visible, indicating exhalation, as noticed by Harrison (1968) in the greenfinch Chloris chloris. The gaping accompanying other stretching movements may be jaw stretching, and gaping during energetic bathing, especially somersaulting, resembles gasping for breath but may be a movement of the jaw to clear the eustachian tubes (cf. Andrew 1956b) after being effected by submergence.

4.4 PREENING MOVEMENTS

4.4.1 Scratching. The head or bill is scratched with the middle claw of the foot which moves rapidly up and down in a fairly fixed arc. The head is lowered towards the foot and positioned according to the point to be scratched. If an extensive area is to be scratched then the head is rotated.

In the experiments scratchings with the left and right feet were distinguished. A single scratching event was considered to end when

FIGURE 4L Scratching.

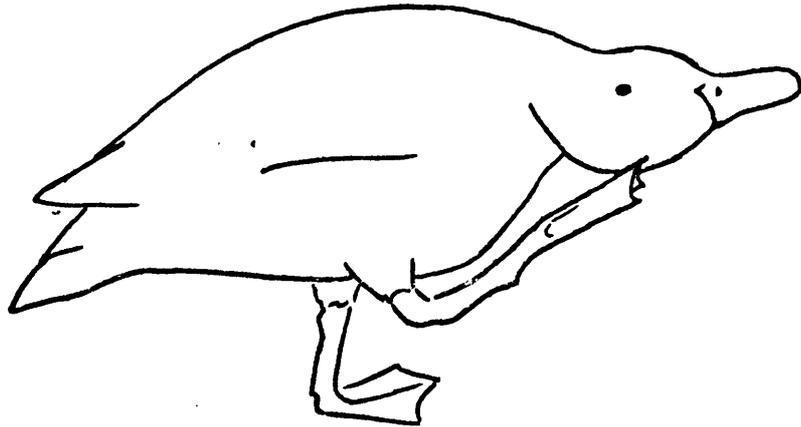
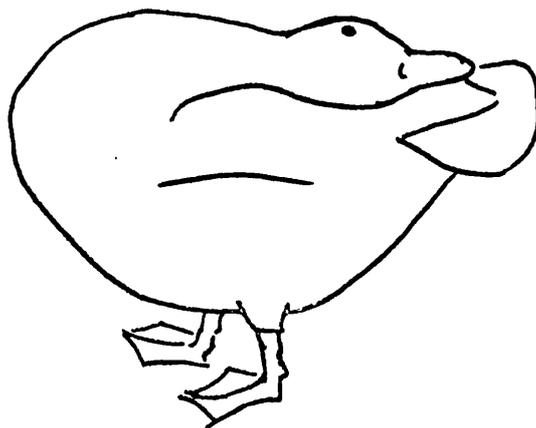


FIGURE 4M Oiling



the claw was noticeably withdrawn from the surface of the head or bill, even if the foot did not touch the ground immediately.

4.4.2 Oiling. This is the movement of taking oil from the uropygial gland. First the gland is nibbled with the bill then the greater part of the head plumage is rubbed over it as the head is rotated over the rump. For this action the tail is cocked sideways toward the head, and the wing on the same side is drooped.

Following McKinney the sequence of preening movements interspersed with oiling and during which oil is spread over the plumage, will be referred to as an oiling-preen. According to McKinney the first oiling in an oiling-preen may consist of only the nibbling of the oil gland with the bill, and subsequent oilings are successively more complete. In my experience oiling does not show such a wide range of intensities as this implies and nibbling the gland without rotating the head on it is rather infrequent.

In the experiments oiling from the left and right sides were distinguished. Each of these movements was recorded as a single event.

4.4.3 Preening and rubbing. Preening is the mandibulation of feathers with the bill. At close range, nibbling at the base of the feathers could possibly be distinguished from drawing them through the bill, from the base to the tip; this distinction was not attempted in the present study.

Rubbing includes rubbing the plumage with the head and wiping it with the closed bill, not infrequently both at the same time; for example, the flanks may be rubbed with the cheek while being wiped with the side of the bill, or the breast may be wiped with the underside of the bill while the back of the head is rubbed on the shoulders.

Not infrequently, a bird appeared to be rubbing the plumage with the head and preening individual feathers at the same time. All such cases were recorded as preening only. Usually the sites being rubbed and preened both fell within the same area, most often "flanks" or "over-the-wings"; if not, only the area being preened was counted.

For the experiments preening and rubbing were broken down into units based broadly upon the area toward which the actions were directed. Divisions of the body surface of other species by other authors (van Iersel and Bol 1958; McFarland and Baher 1968) were unsatisfactory for this purpose. Instead the body surface was divided into areas the limits of which could as far as possible be defined by reference to the plumage pattern and topography of the male Mallard.

Two midline areas were defined - breast and belly. The breast is the chestnut coloured area on the chest of a drake mallard. The belly is the area between the posterior margin of the breast and the thighs. Unfortunately, the latero-dorsal margin of the belly could not be defined so clearly, but it is illustrated in fig. 4N which shows the divisions of the body surface used.

The flank and wing areas are mirrored on each side of the body and accordingly movements directed toward them on the left and right sides of the body are distinguished. Occasionally, part of the right wing, for instance, may be preened from the left, i.e. with the head and neck turned round to the left side. In such cases, the movement was recorded as a "left" or "right" movement depending upon which way the neck was turned round rather than the target area.

The categories of preening and rubbing over-the-wing included as target areas, the shoulders, back and wings as well as the dorsal surface of the wings. Both preening under-the-wing-dorsally and preening

FIGURE 4N Divisions of body surface used in classifying preening.

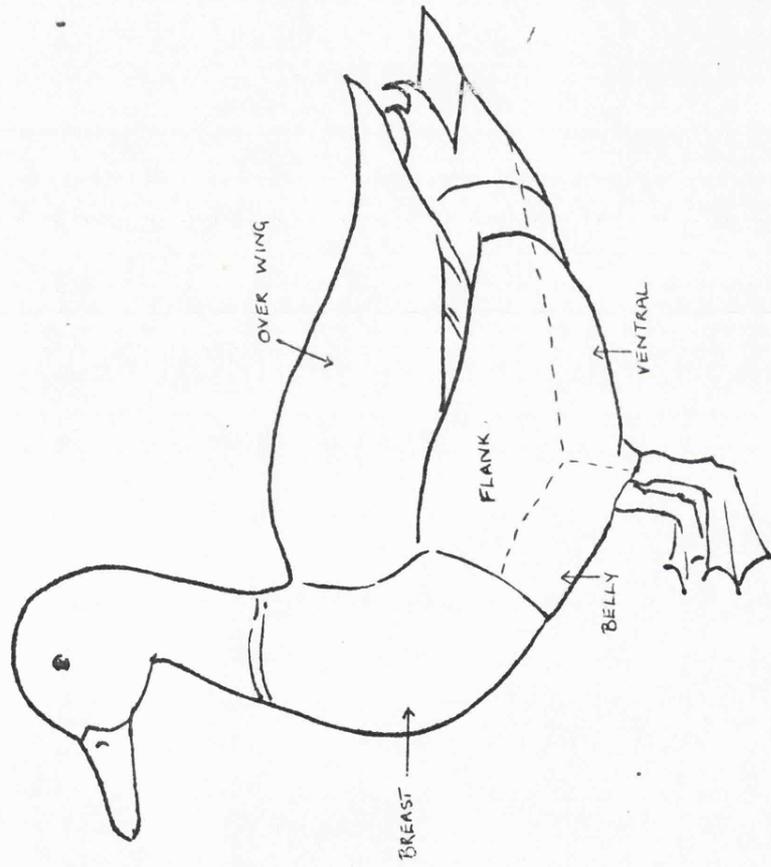


FIGURE 4P Breast preening.

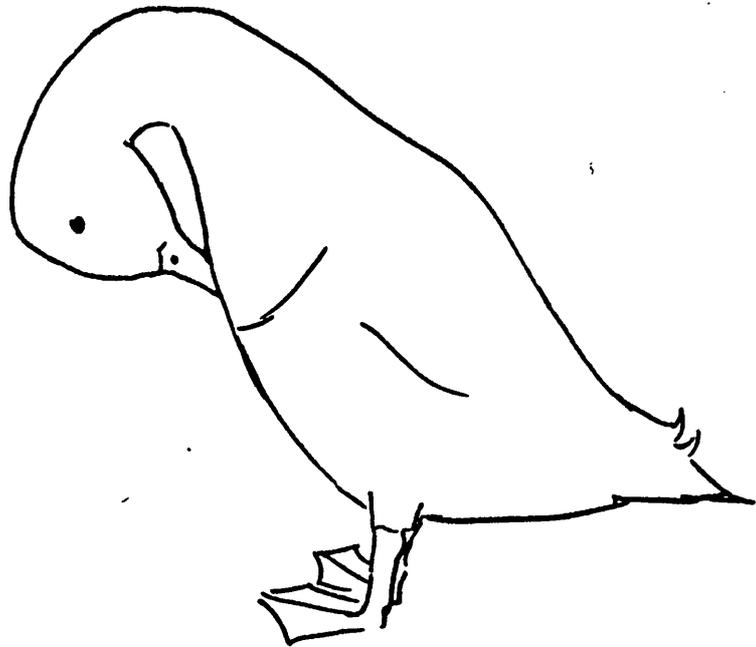


FIGURE 4Q Preening-over-wing.

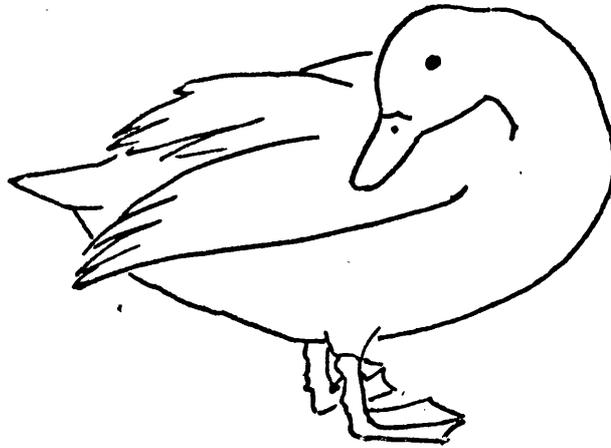


FIGURE 4R Preening-under-wing-dorsally.

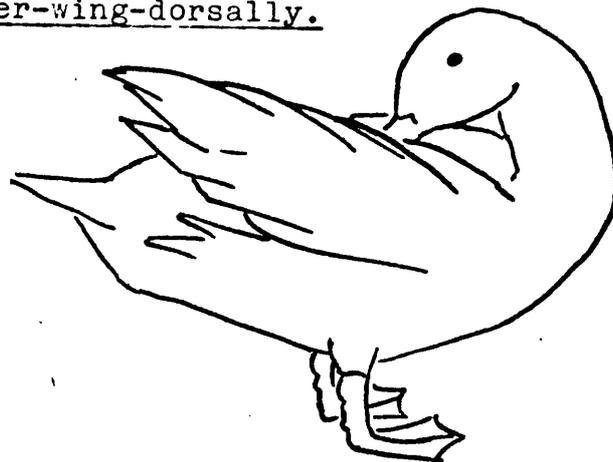


FIGURE 4S Preening-under-wing-ventrally.

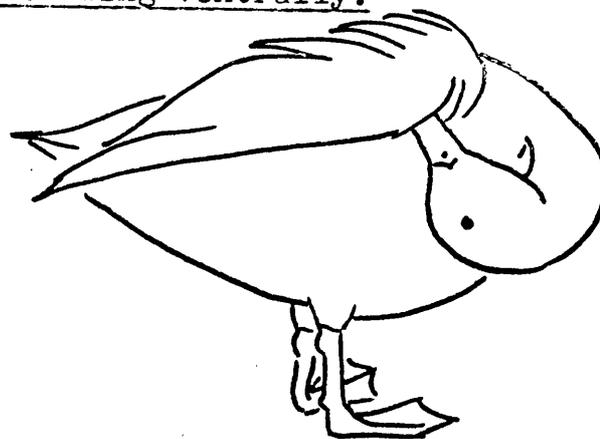
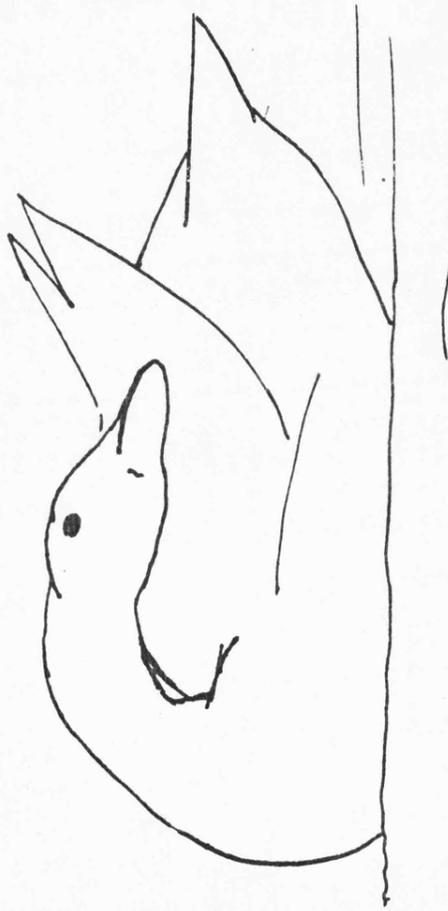


FIGURE 4T Rubbing-over-wing.



under-the-wing-ventrally include preening the body feathers as well as those on the inside of the wing as in many cases it was impossible to distinguish the two. The notation ventrally and dorsally indicates whether the inside of a wing was reached upward from the flanks or downward from the back. Rubbing over-the-wings included what is sometimes called shoulder-rubbing which may have been better treated as a distinct movement: Simmons (1961) suggests that it is a relatively specific response to irritation around the eye.

Preening and rubbing of the flank areas were not distinguished from one another in the experiments.

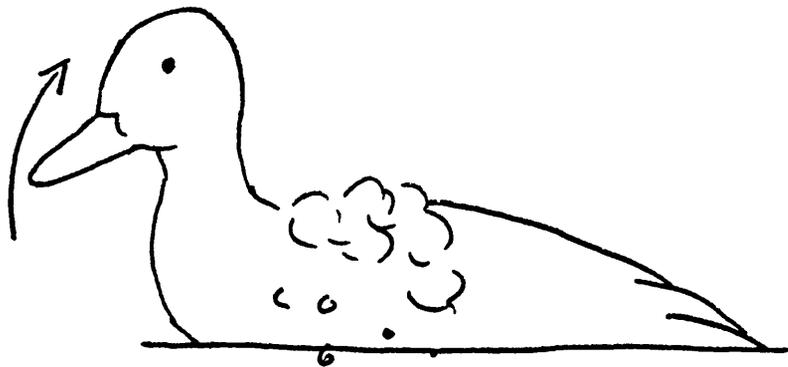
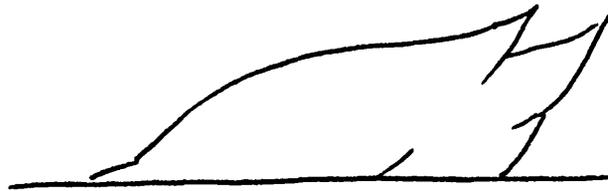
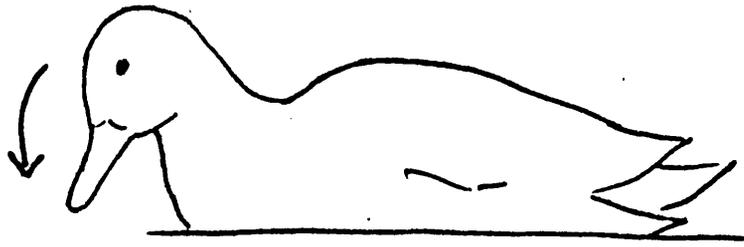
The ventral area is the area on the ventral surface posterior to the thighs, including the region round the cloaca, although it is essentially a midline area, movements directed toward it were distinguished according to whether it was reached from the right or from the left.

4.4.4 Foot-peck. Any unfeathered part of the hind limb may be nibbled with the bill. The term is as used by McKinney. The foot may be lifted up toward the head, to be nibbled as illustrated by McKinney, or it may be nibbled while only slightly raised or on the ground. Although frequently observed, foot-pecking was not recorded in the experiments.

4.5 BATHING MOVEMENTS

4.5.1 Head-dip. In this, the commonest bathing movement, the head is ducked briefly under the water surface of the water, probably always with the bill angled slightly to one side. Water is often scooped over the back as the head is brought out of the water. Head-dips are performed standing on land and in shallow water as well as afloat.

FIGURE 4U Head-dip.



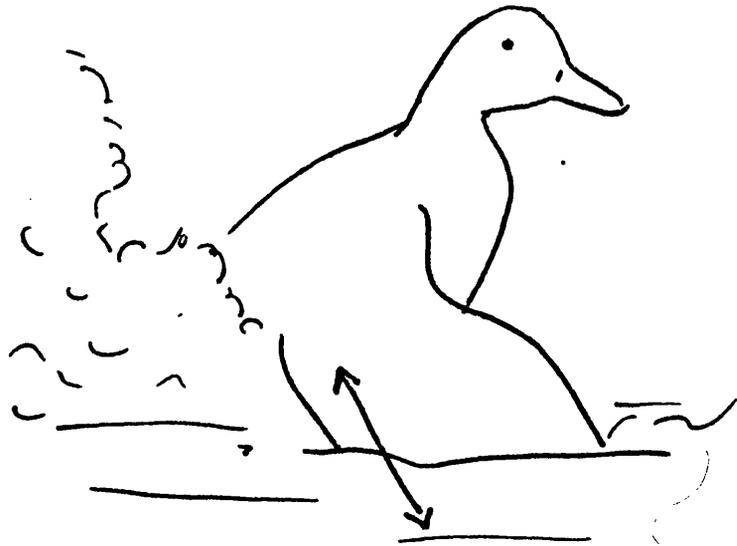
In the experiments, each head-dip was recorded as a single event.

4.5.2 Wing-shuffling. This consists of more or less horizontal movements of the wings over the back, usually associated with head-dipping and tail-wagging. Wing-shuffling should be distinguished from what McKinney called "wing-shuffle-and-tail-fan" (here called wing-twitching). Wing-shuffling was frequently seen in the experiments but not recorded in its own right.

4.5.3 Wing-thrashing. This is a vigorous beating of the wings against the water with the body somewhat reared from the water and leaning slightly to one side. Wing-thrashing was observed only infrequently in the experiments. It was recorded in units of a bout of rapid beats of the wings against the surface of the water. A bout was considered to have ended when a decline in the frequency of beating was accompanied by either the subsiding of the body on to the surface of the water, or a change in the side to which the bird leaned and hence in which wing was beating the water most vigorously. Wing-thrashing usually occurs as wing-shuffling increases in intensity and the changeover point between the two is sometimes rather arbitrary.

4.5.4 Somersaulting. The neck is dipped into the water with the bill pointed upward, quite unlike the initial stages of a head-dip or up-ending to feed. The legs kick the body through the vertical position until the ventral surface is uppermost with the legs in the air. The body is then rolled over sideways until the dorsal surface is uppermost and the bird is in its normal swimming position on the surface of the water but facing the opposite direction to when it started the somersault. As the bird rolls up into the normal position vigorous wing movements have already started and, typically, the somersault grades

FIGURE 4V Wing-thrashing.



into wing-thrashing. Incomplete somersaults are not infrequent - instead of rolling up sideways the bird resumes its normal position by reversing its initial movement about its transverse axis, so finishing facing the same direction as when it started.

Somersaults were never observed in the experiments, although they were seen fairly frequently in free-flying birds, and particularly birds which had been deprived of access to water for some time.

4.5.5 Wallowing. The bird lies motionless with ruffled feathers, low in the water, as if soaking. Wallowing is typical in pauses during high intensity bathing, that is when bathing movements in addition to head-dipping and wing-shuffling are performed. The term "wallowing" is taken from Simmons' (1970) account of bathing in the great crested grebe Podiceps cristatus. Wallowing was not recorded in the experiments.

4.5.6 Dashing-and-diving. (Called diving-play by Leuret 1948). In dashing-and-diving shallow dives alternate with rapid "dashing" over the surface of the water, partly propelled by a rowing action of the wings, with occasional short flights. Fast, sharp turns are performed both on the surface during the dashing and under the water during dives. Dashing-and-diving is socially contagious and strongly reminiscent of escape behaviour. Dashing-and-diving was never seen during the experiments.

4.5.7 Dive-bathing. The bird dives from the surface of the water either immediately before or during bathing activity. I disagree with McKinney who treats diving by solitary anatids as dashing-and-diving. Dive-bathing by individual or paired birds, even in relatively crowded conditions in captivity, seldom has the contagious effect of dashing-and-diving. Other differences between dive-bathing and dashing-and-diving

are: 1, the dashing phase is absent from dive-bathing; 2, birds often wallow between dives in dive-bathing but seldom if ever during dashing-and-diving; 3, dives are somewhat shallower in dashing-and-diving; 4, dive-bathing dives are seldom if ever from flight as in dashing-and-diving. Dive-bathing was not observed during the experiments.

CHAPTER FIVE

THE EXPERIMENTS

5.1 AIM

The aim of the experiments was to discover how general was the effect of increasing peripheral stimulation from relatively localised areas of the body surface on a broad range of comfort movements. Particular questions to be asked were:

1. Would increasing the input from one area of the body surface increase preening directed at that area, and would such an effect be specific in the area treated or generalise to preening directed at other areas?

2. Would the various shaking and bathing movements in the Mallard's repertoire be facilitated to different degrees by increasing the input from different areas of the body surface and, if so, which movements are facilitated by which treatments?

5.2 TECHNIQUE

The problem was to devise an experimental technique to increase the cutaneous input from circumscribed areas of the body surface. It is difficult to obtain localised stimulation with water sprays as have been used in earlier studies. Some other points requiring consideration were as follows:

1. The stimulus would have to be such that its effects were not swamped by handling and other sources of plumage disturbance.

2. The effects of the stimulus would be relatively short-lived.

3. The bird should not be able to transfer appreciable amounts of the stimulus source from one part of the body surface to another, e.g. by preening.

A technique was devised whereby a given area of the plumage was gently brushed with a dilute (1%) solution of a commercial detergent (Teepol L, Shell chemicals) and the bird introduced into a pool where the treated area quickly became saturated with water. Typically, the bird would start bathing and then commence intensive preening. After bathing and preening, and after the plumage had dried out, the bird was able to return to the water showing no visible signs of loss or impairment of water repellency, even if it had not in the interim oiled the plumage with uropygial gland secretion. This fits in with recent work on the water repellency of feathers.

Two factors are thought to be involved in the water repellency of feathers; their fine structure and the preen-oil from the uropygial gland. It is uncertain whether the oil acts directly to waterproof the plumage, or indirectly by preserving feather structure (Clark and Kennedy 1968). In either case it is unlikely that much of the effect of the detergent treatment on water repellency persisted after the detergent had been washed from the feathers by the bird bathing. Clark and Kennedy considered that it is probably extremely difficult to remove all traces of preen-oil from the feathers, and it is unlikely that a very high proportion was removed by the fairly mild treatment used here. The detergent probably changed the surface tension characteristics of the feather-water interface, allowing water to penetrate between the barbules. Such a change would last only until the plumage was washed free of detergent and dried out. There were no signs of any loss of water repellency from areas of the plumage other than that treated. Any transfer of the detergent to other areas of the body surface, e.g. by preening, before the detergent was washed away, must have been minimal.

Subsequent to the experiments it was discovered that Teepol L,

the detergent used in the experiments, had been tested for possible use as a cleaning agent for oiled seabirds (Research Unit on the Rehabilitation of Oiled Seabirds 1971). Feathers soaked in 1% Teepol at 40-45°C and then given three rinses, each for one minute in 50 ml. of tap water resisted wetting even after 24 hours immersion. This detergent is thus very readily rinsed from feathers.

As a control, the appropriate area of the plumage was disturbed with a dry, detergent-free brush, to an extent equivalent to the brushing with detergent. In this way, in the control condition a bird would receive the same amount and type of handling and general plumage disturbance as it received under the treatment condition. Therefore the two conditions would differ only in terms of a localised effect.

5.3 EXPERIMENTAL DESIGN

The number of birds available for any one experiment was rather limited and there were marked individual differences, particularly in the vigour with which the ducks performed comfort behaviour in the experimental situation. For these reasons each subject was used as his own control.

Each bird was tested under experimental and control conditions on successive days. Half the subjects were given the experimental treatment on one day and the control treatment the next. The remaining subjects were treated in the reverse order. Usually, several subjects were tested on any one pair of consecutive days, in which case half these birds were given the two treatments in one order and half in the other. To a large extent this procedure will have guarded against systematic influences of weather and other environmental factors. In addition, testing was abandoned in conditions any more severe than extremely light rain.

The so-called "balanced" repeated measures design used here can lead to erroneous results if the relative effects of the two treatments are altered by the order in which they are administered. For example, a loss of water repellency carried over from the experimental to the control treatment would reduce the apparent difference between the two treatments in terms of movements facilitated by wet plumage. The data were examined for traces of any such carry-over effects on the comfort movements recorded: there were none.

5.4 SUBJECTS

A total of 22 male Mallards in their first, second or third years of life, were used in the experiments. Some had been reared by their parents at the departmental field station, and others had been reared in the laboratory in varying degrees of isolation from other ducks. Previous to the experiments, many of the birds had been free-flying for periods of several weeks. At other times, they were kept in various flight pens.

The birds were fed a mixture of wheat and maize together with various proprietary feeds and supplemented occasionally with fresh vegetable matter and invertebrates. In addition they found a fair amount of natural food themselves.

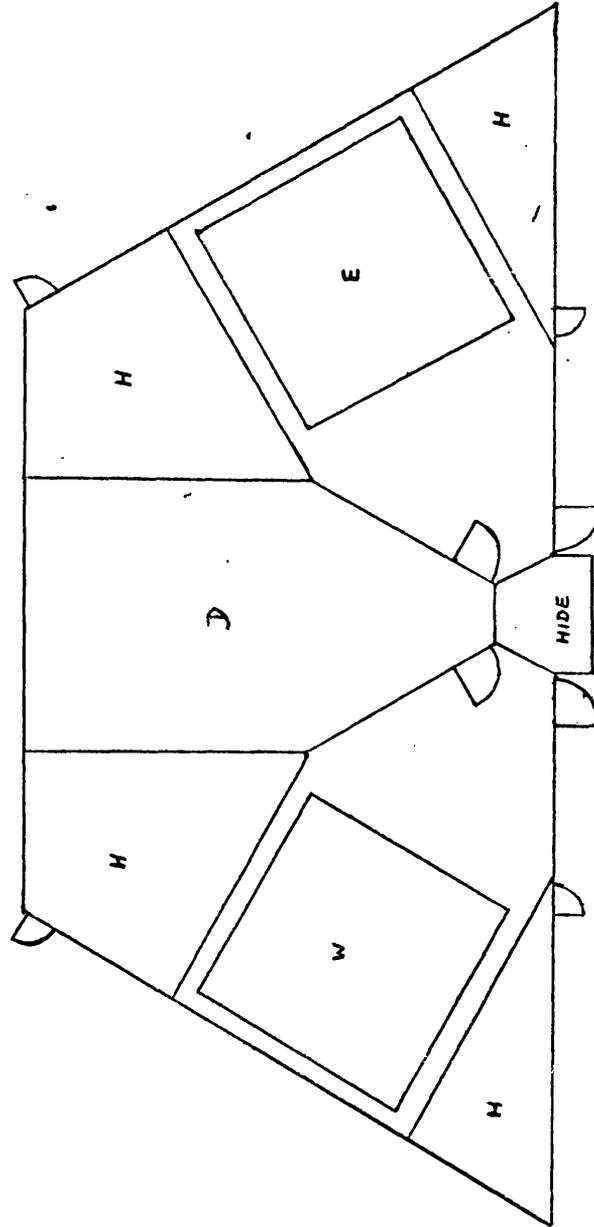
Each bird was marked individually with a numbered metal ring and a combination of colour-rings. Some were also fitted with a pair of nasal discs (Bartonek and Dane 1964) or stained with ICI Durafur. None was pinioned or wing-clipped.

5.5 EXPERIMENTAL PENS (Fig. 5A)

Observations were made from a 3 metre high raised hide, directly

FIGURE 5A Experimental pens.

Observation pens are labelled E and W, holding pens are labelled H.



overlooking three large pens. Access to these pens was through doors adjacent to the hide; access to the hide being from outside the pens. Two of the large pens (E and W) each had a 4.5m. x 4.5m. x 30cm. deep, concrete pool with a 30cm. concrete surround and fitted with a drain. Between these pools and the observation hide was an area of sparsely grassed ground approximately 13.5m². The other large pen (D), of a similar total area (43.5m²) had no concrete pool but a small plastic pond, approximately 1m. x 2m., which was sunk into the ground.

The roof of the pens was made of 5cm. mesh nylon netting, and sloped from 3m. high at the hide to 1.8m. high at the far edge. To reduce disturbance from outside, the block of pens was surrounded by a wooden fence, 180cm. high along the southern side and 120cm. high around the remainder, topped with nylon netting reaching to the roof. The large pens were divided from one another and from the smaller holding pens adjacent, by 45cm. high wooden panels also topped with nylon netting to the roof. Ducks could be driven between pens through intercommunicating doors adjacent to the hide, or through hatchways in the corners of the pens farthest from the hide.

5.6 PROCEDURE

A minimum of seven days was allowed to elapse between experiments on any one individual. Apart from this the ducks used in each experiment were chosen at random from those accessible but not required for observation on their display behaviour, showing no outward signs of moult and otherwise in good condition at the time. Individual birds were used for between one and five experiments.

Between treatments and for at least 24 hours before being used for an experiment, the subjects had access to water in which they could

bathe freely, either in a flight pen across a neck of the field station lake or in one of the two large experimental pens with a pool. Each duck had considerable experience of the experimental pens before being used for an experiment for the first time. Immediately prior to testing, the subjects were herded into either the trap attached to the flight pen, or into the small triangular holding pens in the experimental pen complex. Here they were held until required, when they were caught by hand.

Each subject was taken into the hide and treated, there, with either the detergent or by dry brushing. The bird was immediately released from the hide, through a hatchway two metres above the ground, into one of the large experimental pens with a pool (E or W) where invariably it landed in, or proceeded directly to, the pool.

The subject was observed for fifteen minutes. His behaviour was recorded in detail by means of a verbal commentary into a portable tape recorder. At the same time an auditory time signal at ten second intervals was added to the recording. The recordings were later transcribed into a written format and eventually punched onto data cards. The tape recorded commentary allowed a greater flexibility than the use of an event recorder would have done.

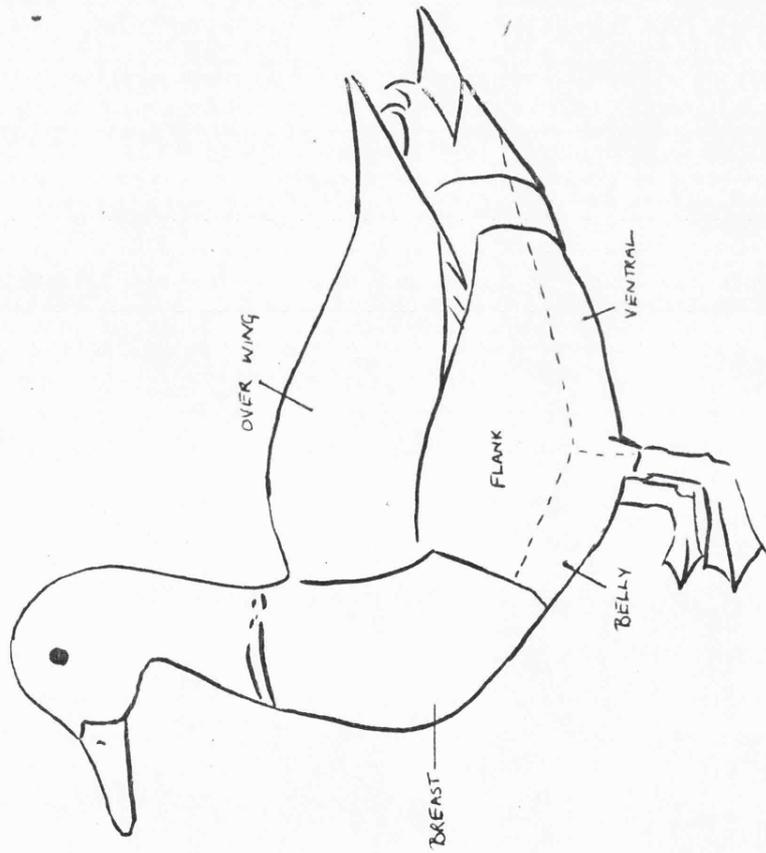
The experimental pools were cleaned, and the water changed, at least between each experiment.

5.7 THE EXPERIMENTS

A total of ten experiments was carried out; these are listed below. Eight subjects were used for each experiment.

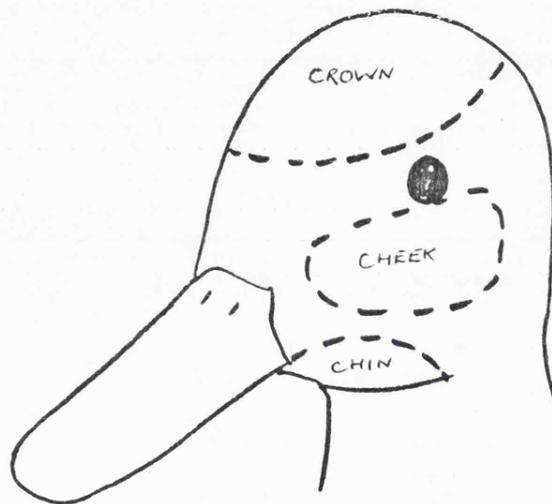
1. Detergent treatment versus dry brushing of the "breast" area (Fig. 58).
2. Detergent treatment versus dry brushing of the "belly" area (Fig. 58).

FIGURE 5B Areas of the body surface.



3. Detergent treatment versus dry brushing of the outer surface of both wings in the folded position; "over-wings" (Fig. 5B).
4. Detergent treatment versus dry brushing of the "crown" area (Fig. 5C).
5. Detergent treatment versus dry brushing of the "cheek" area (Fig. 5C) on one side of the head only. Each subject had the experimental and control treatments on the same side of the head, on the left for half the subjects and on the right for the others.
6. Detergent treatment versus dry brushing of the "chin" area of the head (Fig. 5C).
7. Detergent treatment versus dry brushing of the coverts on the undersides of both wings; "under-wing coverts".
8. Detergent treatment versus dry brushing of both "flanks" (Fig. 5B).
9. Detergent treatment versus dry brushing of the area on the underside of the ducks, between the legs and the anterior margin of the black area under the tail (Fig. 5B); the "ventral" area. The total cumulative duration of tail-wagging, i.e. any lateral to and fro movement of the tail was recorded in the experiment. This precluded consistent recording of many of the other movements; only body-shakes, wing-flaps, head-flicks, oiling and bathing were scored.
10. Detergent treatment versus dry brushing of the ventral area as in experiment 9 except that the tail-wagging components of body-shakes, tail-wagging during bathing and tail-wagging immediately following wing-flapping or preening of the ventral area, were omitted from the timing. In addition to those comfort movements mentioned above as being scored in experiment 9, head-scratching and "elevated-tail-wags" (see 4.2.7) were also recorded.

FIGURE 5C Areas of the head.



CHAPTER SIX

RESULTS 1 : MOVEMENT FREQUENCIES

6.1 INTRODUCTION

To recap, it was desired to assess the effects of stimulating various circumscribed areas of the body surface on a number of the comfort movements described in chapter 4. These effects were analysed by comparing the frequency of occurrence of each activity under the experimental and control conditions in each experiment.

To facilitate the integration of the findings, the results are organised so that all effects on any one movement are brought together. The order of presentation more or less follows that used in chapter 4. The relationship of the findings to the ideas of other workers, especially those of ^{van} Iersel and Bol (1958) and McKinney (1965) will briefly be commented upon movement by movement. In addition, a brief resumé is incorporated immediately after each group of movements has been dealt with; in this way it is hoped to integrate the findings concerned with shaking movements, preening movements and bathing movements. At the end of the chapter, the results are illustrated graphically, experiment by experiment.

Fisher's randomization test for matched-paired data (Siegel 1956, Bradley 1968) was used as the basic statistical technique for this analysis. To save computation time this very laborious test was not used when the application of a sign test indicated a significant effect. The effect of this procedure on the likelihood of making a type I error is minimal and is far outweighed by the computational labour saved.

The working hypothesis initially adopted was that, compared with controls, the experimental treatments would increase the frequency of all movements. Accordingly, one-tailed tests in that direction were employed. If the reverse effect, a decrease, was in fact observed, then its significance was assessed, post hoc, using a two-tailed test.

6.2 ACTIVITIES OTHER THAN COMFORT MOVEMENTS

6.2.1 Time spent in and out of the water

It is useful to consider the amount of time the birds spent in and out of the water in order that we may assess the effects of experimental treatments on movements which by their nature were more likely to be performed while afloat or while on land. Each entry from land into the water and each exit from the water on to land was recorded in experiments 1-8. In no case was the frequency of these actions affected significantly by an experimental treatment. From the raw data the relative time spent in and out of the water was assessed, using an instantaneous sampling technique, as the number of time signals (every ten seconds) when the bird was on land. Only one treatment - of the belly area (experiment 2) - had a significant effect: it increased the time spent on land ($p=.027$, one-tailed randomization test).

6.2.2 Drinking

Drinking was recorded in all experiments as a point event consisting of immersing the bill in the water, withdrawing it and tilting it upward. In no case was its frequency affected by the experimental treatments. This provides supporting evidence that the detergent solution was washed from the feathers before the bird started preening vigorously as preliminary observations gave a very clear indication that ducks reacted to the taste of detergent by drinking repeatedly.

6.2.3 Flying

In all experiments, all flights made by the birds were recorded. Because of the restricted air space in the observation pens, all these flights were necessarily of short duration and they could meaningfully

be treated as unit events bounded by take-off and touch-down. In no case was the frequency of flights significantly affected by an experimental treatment.

6.3 SHAKING MOVEMENTS

6.3.1 Body-shakes (Table 6.1)

In the experiments, body-shakes were significantly increased (compared with controls) by detergent treatment of the breast, belly and ventral areas (experiments 1, 2 and 10 respectively).

Analysed in more detail by subdividing body-shakes into swimming-shakes and standing-shakes, the data show that swimming-shakes were significantly increased by treatment over-the-wings and of the flanks (experiments 3 and 8) as well as by treatment of the breast and belly. Treatment of the ventral area (experiment 10), and the breast, significantly increased standing shakes.

The results support McKinney's suggestion that swimming-shakes are elicited by wetting of the breast, but swimming-shakes are clearly facilitated by wetting of other parts too, including areas of the dorsal surface. In contrast, the evidence suggests that standing-shakes may be elicited primarily by wetting the underside of the body. This apparent difference could possibly be due to the dorsal surface shedding water rapidly, with the underside of the body accumulating water that had trickled down. This would result in a standing bird having a relatively dry back but a wet underside, whereas, in the case of a swimming bird, the dorsal surface would tend to be kept wet, for instance by bathing. However, it is difficult to envisage water being shed quickly enough from the dorsal surface for this factor to explain why experimental wetting over-the-wings failed to facilitate

TABLE 6.1 Mean numbers of body-shakes (per 15 minute observation period).

| <u>experiment</u> | | <u>body</u> <u>-shakes</u> | <u>swimming</u> <u>-shakes</u> | <u>standing</u> <u>-shakes</u> |
|-------------------|------|-------------------------------|-----------------------------------|-----------------------------------|
| 1.breast | cntl | 3.87 | 0.75 | 3.13 |
| | expl | 13.25*** | 7.25** | 6.00* |
| 2.belly | cntl | 4.25 | 0.50 | 3.75 |
| | expl | 13.00* | 5.25*** | 7.75 |
| 3.o.wings | cntl | 5.63 | 1.13 | 4.50 |
| | expl | 6.50 | 2.38* | 4.13 |
| 4.crown | cntl | 3.75 | 0.38 | 3.37 |
| | expl | 4.00 | 0.38 | 3.63 |
| 5.cheeks | cntl | 5.13 | 0.38 | 4.75 |
| | expl | 5.88 | 0.38 | 5.50 |
| 6.chin | cntl | 5.63 | 0 | 5.63 |
| | expl | 6.00 | 0.38 | 5.63 |
| 7.u.wings | cntl | 5.38 | 0.12 | 5.25 |
| | expl | 6.25 | 1.75 | 4.50 |
| 8.flanks | cntl | 4.50 | 0.12 | 4.38 |
| | expl | 7.00 | 3.00** | 4.00 |
| 9.ventral | cntl | 4.75 | 2.38 | 2.38 |
| | expl | 4.88 | 2.00 | 2.88 |
| 10.ventral | cntl | 3.63 | 0.63 | 3.00 |
| | expl | 5.75** | 0.63 | 5.13** |

* : $p \leq 0.05$ (one tailed)

** : $p \leq 0.01$ (one tailed)

*** : $p \leq 0.005$ (one tailed)

standing-shakes.

A further consideration is that, in principle, the lack of a clear indication that both swimming-shakes and standing-shakes are elicited by the same types of peripheral stimulation could have been due to the inevitable inverse relationship between time spent on land and in water. This is unlikely in view of the results reported in section 6.2.1, but to check further this possibility, the analyses were repeated after transforming the frequencies of the two movements to rates per unit time spent in the water or on land. The only change was that, whereas treatment of the breast area significantly increased the number of standing-shakes, the effect on the rate of standing-shakes per unit time on land, fell just short of significance.

Without giving too much weight to negative results, the lack of a marked similarity in the effects of the various treatments on the two movements certainly suggests that it would be wise to retain the standing/swimming distinction as applied to body shakes.

6.3.2 Head-flicks, head-shakes and dip-shakes (Table 6.2)

Head flicks were significantly increased by detergent treatment of the ventral region (experiment 10) and by treatment of the three regions of the head: crown, cheek and chin (experiments 4, 5 and 6).

McKinney suggests that water and foreign bodies are removed from the head by head-flicks and he implies that stimuli from these sources may elicit the movement. The effects of wetting the head fit such an explanation, although the effect of wetting the ventral area is more difficult to understand in these terms unless preening that area involves a particularly large amount of contact between the head and the body plumage, and the head is stimulated by such preening. It is a little

TABLE 6.2 Mean numbers of head-flicks, head-shakes and dip-shakes (per 15 minute observation period).

| <u>experiment</u> | | <u>head-</u> <u>flicks</u> | <u>head-</u> <u>shakes</u> | <u>dip-</u> <u>shakes</u> |
|-------------------|------|-------------------------------|-------------------------------|------------------------------|
| 1.breast | cntl | 8.38 | 45.00 | |
| | expl | 7.50 | 59.00 | |
| 2.belly | cntl | 5.00 | 25.63 | |
| | expl | 2.88 | 43.75* | |
| 3.o.wings | cntl | 7.00 | 29.25 | |
| | expl | 7.38 | 49.38* | |
| 4.crown | cntl | 6.50 | 24.75 | |
| | expl | 28.50* | 23.25 | |
| 5.cheek | cntl | 5.88 | 31.50 | |
| | expl | 25.88*** | 39.13 | |
| 6.chin | cntl | 6.38 | 32.63 | |
| | expl | 28.37*** | 28.62 | |
| 7.u.wings | cntl | 5.25 | 35.75 | 0.25 |
| | expl | 6.50 | 94.63*** | 6.88* |
| 8.flanks | cntl | 3.75 | 26.87 | 0.25 |
| | expl | 4.63 | 61.25** | 4.50* |
| 9.ventral | cntl | 6.00 | | |
| | expl | 7.38 | | |
| 10.ventral | cntl | 4.50 | | |
| | expl | 9.13** | | |

* : $p \leq 0.05$ (one tailed)

** : $p \leq 0.01$ (one tailed)

*** : $p \leq 0.005$ (one tailed)

difficult to envisage, however, why this should be so for the ventral area but not for other regions on the underside of the bird.

Head-shakes were significantly increased by treatment of the belly, over-the-wings, under-the-wings and flanks (experiments 2, 3, 7 and 8).

Clearly, the effects of the treatments upon head-shakes were markedly different from the effects upon head-flicks. Head-shakes were not elicited by wetting the head. McKinney suggests that head-shakes occur in response to foreign bodies on the bill. It seems likely that when head-shakes were increased by experimental wetting of the plumage via detergent treatment, the effect was an indirect result from increased preening in response to wetting (see section 6.4) which in turn provided the stimuli for head-shaking: probably dirt, water or feathers on the bill. On the other hand, as we shall see in the next chapter, head-shaking tended to precede preening rather than follow it. However, it is pertinent to note that treatment of the head, which resulted in extra head-scratching (section 6.4.1), rather than extra preening with the bill, did not significantly increase head-shaking.

According to ^{Van}Iersel and Bol "the occurrence of head-shaking is influenced by the external situation of 'being wet'". They present data which show that, in brooding Sandwich Terns, head-shaking is more frequent in rain than during dry weather. Rain did not seem to affect the frequency of the other comfort movements that they recorded. It seems likely that head-shakes were performed in response to water droplets on the bill rather than water droplets on the body surface as a whole.

Dip-shakes were distinguished from head-shakes that closely followed a bill-dip, only in experiments 7 and 8. Treatment of the under-wing-

coverts and of the flank significantly increased dip-shakes in these experiments. These results give little information about the causation of dip-shakes but they may be elicited by stimuli similar to those eliciting head-shakes.

6.3.3 Bill-dips (Table 6.3)

Bill-dips were significantly increased by treatment of the belly and under-wing-coverts (experiments 2 and 7). Bill-dipping probably serves to remove foreign bodies from the bill, as suggested by McKinney, and the stimuli from such bodies, which must often occur during preening, may well elicit the movements. Bill-dips also occur before bathing, perhaps as incipient head-dips. Nonetheless, it is difficult to understand why bill-dips should be facilitated, even indirectly through preening or bathing, by treatment of the belly and under-the-wings while treatment of other areas showed no significant effect.

6.3.4 Tail-wags (Table 6.4)

Tail-wags were only recorded in experiments 9 and 10 when the ventral area received the experimental treatment. As explained in section 4.2.7, tail-wagging was scored by its cumulative duration. In experiment 9 the total time during which there was any to-and-fro movement of the tail was recorded. By this measure, detergent treatment was found to significantly increase tail-wagging. This effect could have been due to the facilitation of activities closely associated with tail-wags or activities which include lateral movements of the tail as an integral part. To exclude this possibility, in experiment 10 the time spent tail-wagging was recorded omitting instances of tail-wagging associated with body-shakes, wing-flaps, bathing, or preening directed at the ventral area. With this restriction the amount of tail-wagging

TABLE 6.3 Mean numbers of bill-dips (per 15 minute observations period).

| <u>experiment</u> | | <u>number of bill-dips</u> |
|-------------------|------|----------------------------|
| 1.breast | cntl | 10.00 |
| | expl | 8.63 |
| 2.belly | cntl | 6.13 |
| | expl | 18.00* |
| 3.o.wings | cntl | 6.50 |
| | expl | 6.63 |
| 4.crown | cntl | 5.38 |
| | expl | 6.13 |
| 5.cheek | cntl | 6.88 |
| | expl | 8.25 |
| 6.chin | cntl | 5.38 |
| | expl | 5.25 |
| 7.u.wings | cntl | 8.38 |
| | expl | 21.25* |
| 8.flanks | cntl | 7.00 |
| | expl | 7.75 |

* : $p \leq 0.05$ (one tailed)

TABLE 6.4 Mean durations of tail-wagging and mean numbers of elevated tail-wags (per 15 minute observation period).

| | |
|------------------------------|---|
| <u>experiment 9.ventral</u> | <u>duration of tail-wagging(entire¹)</u> |
| cntl | 65.88 secs |
| expl | 136.00 secs * |
| | |
| <u>experiment 10.ventral</u> | <u>duration of tail-wagging(restricted¹)</u> |
| cntl | 21.88 secs ¹ |
| expl | 54.13 secs *** |
| | |
| <u>experiment 10.ventral</u> | <u>number of elevated tail-wags</u> |
| cntl | 2.25 |
| expl | 9.63 * |

* : $p \leq 0.05$ (one tailed)

*** : $p \leq 0.005$ (one tailed)

1 : see text for explanation of restricted and entire timing of tail-wags.

was still significantly increased by the treatment. Also in experiment 10, the elevated tail-wags described in section 4.2.7 were counted. These too were found to be significantly increased by detergent treatment of the ventral area.

McKinney suggests that tail-wagging may occur as a direct response to water on the tail, but noted that it often occurs when the tail itself is not wet. At least some of these instances might be due to wetting or disturbance of the ventral area.

6.3.5 Wing-flaps (Table 6.5)

Wing-flaps were significantly increased by treatment of the flanks, over-the-wings and the under-wing coverts (experiments 3, 7 and 8). Separating wing-flaps into standing-flaps and swimming-flaps, it was found that swimming-flaps were significantly increased by treatment of the flanks and over-the-wings. Treatment of the chin (experiment 6) significantly decreased swimming-flaps. Standing-flaps were not increased significantly in any of the experiments.

McKinney suggested that some wing-flaps may be given in response to moisture on the wings. This would explain why wetting the wings would facilitate wing-flapping. It is not unreasonable, moreover, to suggest that ducks could also wing-flap in response to wet flanks.

The effect of wetting the chin in reducing the frequency of wing-flaps is not easily understood. And it was most unexpected, and puzzling, that none of the treatments facilitated standing-flaps.

As with body-shakes, there is the possibility that the lack of similarity between swimming- and standing-flaps, in terms of the stimuli effective in facilitating the two movements, could have been due to the inverse relationship between the time spent on land and the time spent

TABLE 6.5 Mean numbers of wing-flaps (per 15 minute observation period).

| <u>experiment</u> | | <u>wing-</u> <u>flaps</u> | <u>swimming</u> <u>-flaps</u> | <u>standing</u> <u>-flaps</u> |
|-------------------|------|------------------------------|----------------------------------|----------------------------------|
| 1.breast | cntl | 4.38 | 3.25 | 1.13 |
| | expl | 3.63 | 2.50 | 1.13 |
| 2.belly | cntl | 3.50 | 2.50 | 1.00 |
| | expl | 3.63 | 3.13 | 0.50 |
| 3.o.wings | cntl | 3.50 | 2.75 | 0.75 |
| | expl | 5.13* | 4.25* | 0.87 |
| 4.crown | cntl | 2.13 | 1.25 | 0.87 |
| | expl | 2.38 | 1.75 | 0.62 |
| 5.cheeks | cntl | 2.88 | 1.88 | 1.00 |
| | expl | 3.37 | 1.88 | 1.50 |
| 6.chin | cntl | 3.63 | 3.00 | 0.62 |
| | expl | 2.63 | 1.75+ | 0.87 |
| 7.u.wings | cntl | 4.00 | 1.50 | 2.50 |
| | expl | 6.50 | 4.25** | 2.25 |
| 8.flanks | cntl | 2.13 | 1.38 | 0.75 |
| | expl | 5.25* | 4.00*** | 1.25 |
| 9.ventral | cntl | 3.75 | 2.50 | 1.25 |
| | expl | 4.00 | 3.13 | 0.88 |
| 10.ventral | cntl | 3.25 | 2.00 | 1.25 |
| | expl | 5.75 | 2.38 | 3.38 |

* : $p \leq 0.05$ (one tailed)

** : $p \leq 0.01$ (one tailed)

*** : $p \leq 0.005$ (one tailed)

+ : $p \leq 0.05$ (two-tailed)

afloat. Again, transforming the frequencies of the two movements to rates per unit time spent in the appropriate medium, produced little change in the picture. It became apparent that treatment of the belly area (experiment 2) significantly increased the rate of swimming-flaps per unit time in the water.

Clearly, as with body-shakes, the results support the retention of the distinction between the swimming- and standing- forms of wing-flap.

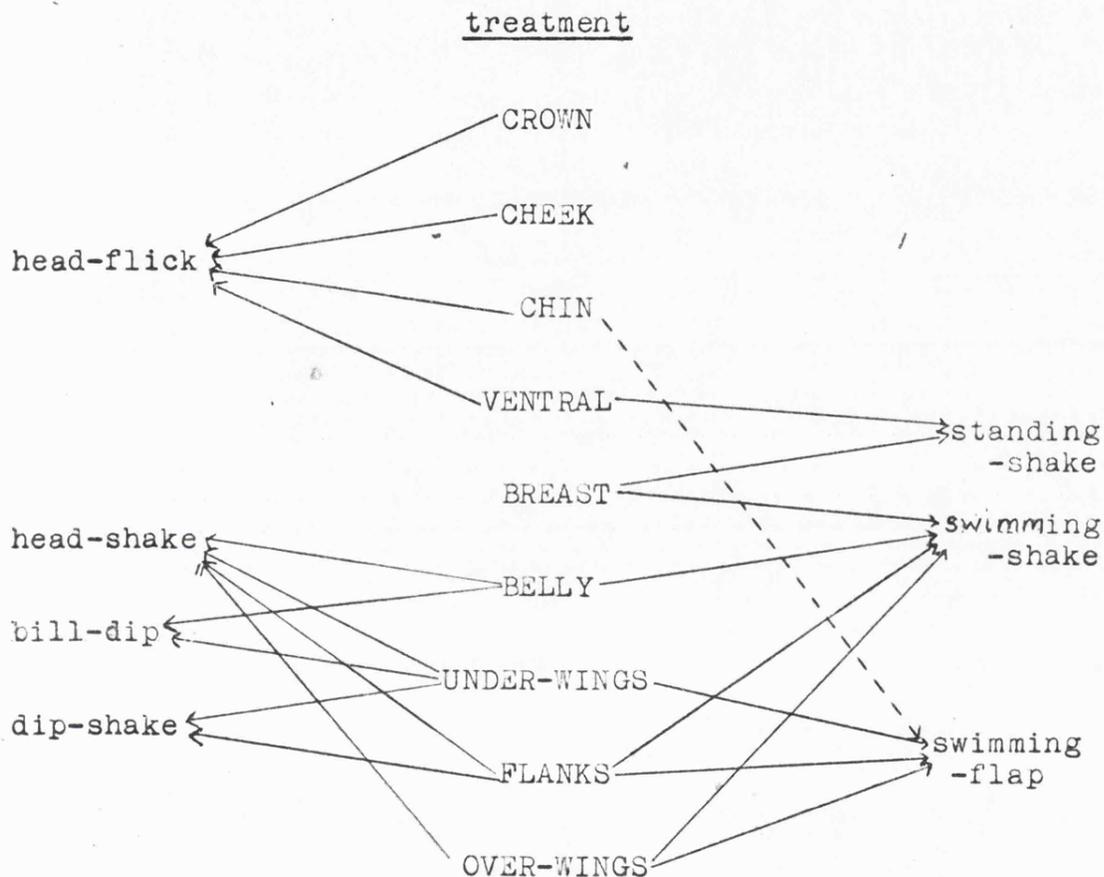
6.3.6 Shaking movements - general comments

Figure 6A gives a diagrammatic representation of the facilitatory relationships, shown by the experiments, between treatment of various areas of the body surface and the performance of the various shaking movements. It is not clear how such results could fit a model whereby the various movements are elicited by qualitatively similar causal factors; if that were the case there should probably be more indication that one kind of experimental stimulus could facilitate most types of movement (but see section 6.2). There is a tendency toward a topographical mapping of the various shaking movements on to separate areas of the body surface. Possibly, more precise techniques of stimulation would show more precise stimulus-response relationships.

The likelihood that head-shakes were facilitated indirectly, via preening, has already been alluded to (6.3.2). The sequential linkage preen to head-shake is very common and is probably controlled in the manner of a stimulus-response chaining mechanism (Hinde and Stevenson 1969) whereby the action of preening produces stimuli on the bill which, in turn, elicit head-shaking. Another frequently observed sequential linkage is wing-flap to head-flick. Commenting on this, McKinney suggested that the coupling of the two movements might have a "central"

FIGURE 6A Relationships between experimental treatments and the frequencies of shaking movements.

Solid line indicates a facilitatory relationship, broken line an inhibitory one.



note: tail-wags are not depicted in this figure. Dip-shakes were distinguished only in the 'under-wings' and 'flanks' experiments (see text).

causal basis. In this respect it is worth noting that none of the three treatments which facilitated swimming-flaps also facilitated head-flicks. If the linkage between the two movements involves common causal factors then peripheral stimulation of the sort manipulated in the experiments would appear to contribute little to this. There remains the possibility though, of stimulus-response chaining with the neck feathers being ruffled during wing-flapping and this eliciting a head-flick.

6.4 PREENING MOVEMENTS

For each category of preening movement, the effects of the experimental treatments were examined, firstly on the category as a whole, and then with the category divided according to the side of the animal's body toward which the action was directed. In the case of experiment 5, involving unilateral treatment of the cheek, the division is of the treated and untreated side of the animals; in the remainder of the experiments the division was left and right sides of the body.

No preening movements were recorded in experiments 9 and 10 in which the ventral area was treated. These experiments will not, therefore, be mentioned in this section.

6.4.1 Scratching (Table 6.6)

Scratching was significantly increased by treatment of the crown, cheek and chin areas of the head in experiments 4, 5 and 6. Scratching from both left and right sides was facilitated by the crown and chin treatments. The cheek treatment significantly increased only scratching with the foot corresponding to the side of the head that was treated.

TABLE 6.6 Mean number of scratches (per 15 minute observation period).

| <u>experiment</u> | | <u>all</u> <u>scratches</u> | <u>scratch</u> <u>-left</u> | <u>scratch</u> <u>-right</u> |
|-------------------|------|--------------------------------|--------------------------------|---------------------------------|
| 1.breast | cntl | 3.37 | 1.75 | 1.63 |
| | expl | 3.37 | 1.75 | 1.63 |
| 2.belly | cntl | 1.75 | 0.75 | 1.00 |
| | expl | 1.25 | 0.50 | 0.75 |
| 3.o.wings | cntl | 0.25 | 0.12 | 0.12 |
| | expl | 1.38 | 1.00 | 0.38 |
| 4.crown | cntl | 1.50 | 0.87 | 0.62 |
| | expl | 16.25** | 8.25** | 8.00* |
| 6.chin | cntl | 2.75 | 1.63 | 1.13 |
| | expl | 12.13* | 5.50* | 6.63* |
| 7.u.wings | cntl | 2.00 | 1.00 | 1.00 |
| | expl | 2.00 | 0.75 | 1.25 |
| 8.flanks | cntl | 1.50 | 0.75 | 0.75 |
| | expl | 0.87 | 0.62 | 0.25 |
| 10.ventral | cntl | 0.63 | 0.25 | 0.38 |
| | expl | 0.75 | 0.25 | 0.50 |
| | | <u>all</u> | <u>trmt.side</u> | <u>non-trmt.side</u> |
| 5.cheek | cntl | 1.25 | 0.62 | 0.62 |
| | expl | 14.25*** | 13.38*** | 0.87 |

* : $p \leq 0.05$ (one tailed)** : $p \leq 0.01$ (one tailed)*** : $p \leq 0.005$ (one tailed)

6.4.2 Oiling (Table 6.7)

In the experiments, treatment of the breast and flank areas (experiments 1 and 8) significantly increased oiling. The effect of the former treatment was significant only for oiling from the right side, while the latter treatment yielded a significant result for oiling from both right and left sides.

6.4.3 Preening-over-the-wings (Table 6.8)

Preening-over-the-wings was not significantly increased by the experimental treatments in any of the experiments, although treatment of the breast area (experiment 1) significantly decreased preening-over-the-wings. Separating preening from the left and right sides, both were significantly decreased by treatment of the breast; in addition, treatment of the belly area in experiment 2 decreased preening over the left wing.

It was expected that, in experiment 3, treatment over-the-wings would facilitate preening-over-the-wings. In fact, the trend in this direction is quite clear, the results falling just short of significance:

All preening over the wings : $p = .055$;

Preening over the left wing : $p = .055$;

Preening over the right wing : $p = .062$.

(All by matched pairs randomisation test.)

6.4.4 Rubbing-over-the-wings (Table 6.9)

In the experiments, rubbing-over-the-wings was significantly increased by treatment of the crown in experiment 4 and significantly decreased by treatment of the flanks (experiment 8). Rubbing-over-both left and right wings was increased by the crown treatment.

TABLE 6.7 Mean numbers of oilings (per 15 minute observation period).

| <u>experiment</u> | | <u>all</u> <u>oiling</u> | <u>oil-</u> <u>left</u> | <u>oil-</u> <u>right</u> |
|-------------------|------|-----------------------------|----------------------------|-----------------------------|
| 1.breast | cntl | 2.63 | 1.63 | 1.00 |
| | expl | 4.63* | 2.38 | 2.25* |
| 2.belly | cntl | 1.75 | 0.87 | 0.87 |
| | expl | 3.00 | 1.38 | 1.63 |
| 3.o.wings | cntl | 1.63 | 0.87 | 0.75 |
| | expl | 2.75 | 1.13 | 1.63 |
| 4.crown | cntl | 1.75 | 0.87 | 0.87 |
| | expl | 1.88 | 0.87 | 1.00 |
| 6.chin | cntl | 2.63 | 1.50 | 1.13 |
| | expl | 2.63 | 1.38 | 1.25 |
| 7.u.wings | cntl | 4.25 | 2.25 | 2.00 |
| | expl | 3.75 | 1.75 | 2.00 |
| 8.flanks | cntl | 3.37 | 1.75 | 1.63 |
| | expl | 5.13* | 2.88* | 2.25 |
| 9.ventral | cntl | 2.13 | 1.00 | 1.13 |
| | expl | 4.25 | 2.38 | 1.88 |
| 10.ventral | cntl | 2.50 | 1.38 | 1.13 |
| | expl | 4.75 | 2.38 | 2.38 |
| | | <u>all</u> | <u>trmt.side</u> | <u>non-trmt.side</u> |
| 5.cheek | cntl | 2.25 | 0.87 | 1.38 |
| | expl | 2.50 | 1.25 | 1.25 |

* : $p \leq 0.05$ (one tailed)

TABLE 6.8 Mean numbers of preen-over-wing (per 15 minute observation period).

| <u>experiment</u> | | <u>preen-</u> <u>o.wings</u> | <u>preen-</u> <u>o.wing-L</u> | <u>preen-</u> <u>o.wing-R</u> |
|-------------------|------|---------------------------------|----------------------------------|----------------------------------|
| 1.breast | cntl | 15.00 | 7.50 | 7.50 |
| | expl | 6.88+ | 3.13+ | 3.75+ |
| 2.belly | cntl | 8.75 | 5.00 | 3.75 |
| | expl | 3.25 | 1.50+ | 1.75 |
| 3.o.wings | cntl | 13.50 | 6.75 | 6.75 |
| | expl | 38.75 | 23.00 | 15.75 |
| 4.crown | cntl | 6.25 | 2.88 | 3.37 |
| | expl | 6.13 | 4.00 | 2.13 |
| 6.chin | cntl | 8.38 | 4.13 | 4.25 |
| | expl | 3.75 | 2.00 | 1.75 |
| 7.u.wings | cntl | 15.13 | 8.75 | 6.38 |
| | expl | 12.13 | 6.13 | 6.00 |
| 8.flanks | cntl | 8.00 | 4.50 | 3.50 |
| | expl | 3.63 | 2.75 | 0.87 |
| | | <u>all</u> | <u>trmt.side</u> | <u>non-trmt.side</u> |
| 5.cheek | cntl | 4.75 | 2.13 | 2.63 |
| | expl | 9.00 | 3.50 | 5.50 |

+ : $p \leq 0.05$ (two tailed)

TABLE 6.9 Mean numbers of rub-over-wing (per 15 minute observation period).

| <u>experiment</u> | | <u>rub-over</u> <u>-wings</u> | <u>rub-over</u> <u>-L-wing</u> | <u>rub-over</u> <u>-R-wing</u> |
|-------------------|------|----------------------------------|-----------------------------------|-----------------------------------|
| 1.breast | cntl | 3.63 | 1.88 | 1.75 |
| | expl | 2.75 | 0.87 | 1.88 |
| 2.belly | cntl | 6.88 | 3.37 | 3.50 |
| | expl | 1.25 | 0.75 | 0.50 |
| 3.o.wings | cntl | 2.13 | 0.75 | 1.38 |
| | expl | 5.75 | 3.00 | 2.75 |
| 4.crown | cntl | 6.75 | 3.75 | 3.00 |
| | expl | 21.00* | 10.50* | 10.50* |
| 6.chin | cntl | 10.63 | 5.75 | 4.88 |
| | expl | 9.00 | 4.38 | 4.63 |
| 7.u.wings | cntl | 12.13 | 6.25 | 5.88 |
| | expl | 6.63 | 3.00 | 3.63 |
| 8.flanks | cntl | 12.75 | 6.88 | 5.88 |
| | expl | 5.50+ | 3.13 | 2.38 |
| | | <u>all</u> | <u>trmt.side</u> | <u>non-trmt.side</u> |
| 5.cheek | cntl | 10.00 | 4.38 | 5.63 |
| | expl | 16.63 | 10.75* | 5.88 |

* : $p \leq 0.05$ (one tailed)

+ : $p \leq 0.05$ (two tailed)

Furthermore, (experiment 5) rubbing-over-the-wing corresponding to the side on which the cheek was treated, was significantly increased by the experimental treatment.

6.4.5 Preening-under-the-wings-dorsally (Table 6.10)

Preening-under-the-wings from a dorsal direction was significantly affected only by treatment of the chin (experiment 6) which significantly decreased the frequency of this action. Taking preening under the left and right wings separately, only the latter was reduced. It had been expected that treatment under the wing in experiment 7 would facilitate this movement; the relevant probability values are as follows:

| | | |
|--|---|-----------|
| Preening under the wings dorsally, both sides | : | p = .074; |
| Preening under the left wing dorsally | : | p = .141; |
| Preening under the right wing dorsally | : | p = .082. |

(All by matched pairs randomisation test.)

In each case the effect was in the predicted direction.

6.4.6 Preening-under-the-wings-ventrally (Table 6.11)

Preening-under-the-wings-ventrally was significantly affected only by treatment under the wings in experiment 7. Preening under both left and right wings were similarly affected.

6.4.7 Preening the flanks (Table 6.12)

Only treatment of the flanks (experiment 8) had a significant effect on preening the flanks. Preening from both right and left sides were similarly affected.

TABLE 6.10 Mean numbers of preen-under-wing-dorsally
(per 15 minute observation period).

| <u>experiment</u> | | <u>preen-u.wings</u> | <u>preen-u.wing</u> | <u>preen-u.wing</u> |
|-------------------|------|----------------------|---------------------|----------------------|
| | | <u>-dorsally</u> | <u>-dorsally-L</u> | <u>-dorsally-R</u> |
| 1.breast | cntl | 4.88 | 2.75 | 2.13 |
| | expl | 2.88 | 1.25 | 1.63 |
| 2.belly | cntl | 6.00 | 3.00 | 3.00 |
| | expl | 0.87 | 0.62 | 0.25 |
| 3.o.wings | cntl | 6.50 | 3.25 | 3.25 |
| | expl | 6.63 | 4.00 | 2.63 |
| 4.crown | cntl | 4.25 | 2.38 | 1.88 |
| | expl | 5.75 | 3.13 | 2.63 |
| 6.chin | cntl | 6.63 | 3.87 | 2.75 |
| | expl | 3.50+ | 2.25 | 1.25+ |
| 7.u.wings | cntl | 14.63 | 7.63 | 7.00 |
| | expl | 30.75 | 15.50 | 15.25 |
| 8.flanks | cntl | 9.38 | 5.13 | 4.25 |
| | expl | 4.88 | 3.25 | 1.63 |
| | | <u>all</u> | <u>trmt.side</u> | <u>non-trmt.side</u> |
| 5.cheek | cntl | 5.13 | 2.38 | 2.75 |
| | expl | 6.25 | 2.38 | 3.87 |

+ : $p \leq 0.05$ (two tailed)

TABLE 6.11 Mean numbers of preen-under-wing-ventrally
(per 15 minute observation period).

| <u>experiment</u> | | <u>preen-u.wings</u> <u>-ventrally</u> | <u>preen-u.wing-</u> <u>ventrally-L</u> | <u>preen-u.wing-</u> <u>ventrally-R</u> |
|-------------------|------|---|--|--|
| 1.breast | cntl | 0.38 | 0.25 | 0.12 |
| | expl | 0.38 | 0.38 | - |
| 2.belly | cntl | 1.13 | 0.50 | 0.62 |
| | expl | 0.25 | 0.12 | 0.12 |
| 3.o.wings | cntl | 1.50 | 0.62 | 0.87 |
| | expl | 2.00 | 1.75 | 0.25 |
| 4.crown | cntl | 1.38 | 1.00 | 0.38 |
| | expl | 2.13 | 1.25 | 0.87 |
| 6.chin | cntl | 0.50 | 0.25 | 0.25 |
| | expl | 0.12 | 0.12 | - |
| 7.u.wings | cntl | 3.50 | 2.00 | 1.50 |
| | expl | 44.50*** | 18.37*** | 26.13*** |
| 8.flanks | cntl | 1.50 | 0.87 | 0.62 |
| | expl | 1.88 | 1.63 | 0.25 |
| | | <u>all</u> | <u>trmt.side</u> | <u>non-trmt.side</u> |
| 5.cheek | cntl | 1.13 | 0.12 | 1.00 |
| | expl | 2.13 | 1.50 | 0.62 |

*** : $p \leq .005$

TABLE 6.12 Mean numbers of preen-flanks (per 15 minute observation period).

| <u>experiment</u> | | <u>preen-</u> <u>flanks</u> | <u>preen-L</u> <u>-flank</u> | <u>preen-R</u> <u>flank</u> |
|-------------------|------|--------------------------------|---------------------------------|--------------------------------|
| 1.breast | cntl | 22.13 | 12.38 | 9.75 |
| | expl | 17.00 | 9.25 | 7.75 |
| 2.belly | cntl | 13.25 | 6.38 | 6.88 |
| | expl | 14.63 | 8.00 | 6.63 |
| 3.o.wings | cntl | 14.00 | 6.75 | 7.25 |
| | expl | 17.25 | 8.50 | 8.75 |
| 4.crown | cntl | 9.50 | 5.63 | 3.87 |
| | expl | 9.88 | 5.25 | 4.63 |
| 6.chin | cntl | 17.88 | 8.75 | 9.13 |
| | expl | 25.13 | 12.38 | 12.75 |
| 7.u.wings | cntl | 25.00 | 13.13 | 11.88 |
| | expl | 16.63 | 8.00 | 8.63 |
| 8. flanks | cntl | 23.88 | 11.25 | 12.63 |
| | expl | 92.75*** | 55.88*** | 36.88*** |
| | | <u>all</u> | <u>trmt.side</u> | <u>non-trmt.side</u> |
| 5.cheek | cntl | 15.50 | 7.38 | 8.13 |
| | expl | 20.25 | 10.63 | 9.63 |

*** : $p \leq 0.005$

6.4.8 Preening the ventral area (Table 6.13)

Preening of the ventral area was not significantly increased by any of the experimental treatments. It was, however, decreased by treatment of the flanks in experiment 8, a finding which held for preening the ventral area from the right but not from the left. Preening of this area was not recorded in the ventral treatment experiments, for reasons already given.

6.4.9 Preening of the breast and belly areas (Table 6.14)

Preening of the breast was significantly increased by treatment of the breast area (experiment 1) and significantly decreased by treatment of the flanks (experiment 8).

Preening of the belly area was significantly increased by treatment of the belly area (experiment 2) and significantly decreased by treatment under the wings (experiment 7).

6.4.10 Preening movements - general comments

Figure 6B gives a diagrammatic relationship of the facilitatory effects of the experimental treatments on the various preening movements. As with shaking movements, a tendency for particular treatments to facilitate particular preening movements was clearly apparent. Specifically, treatment of an area of the plumage facilitated preening of that area or, in the case of treatments of the crown, cheek and chin areas, head-scratching.

It is of interest that treatments of areas on the head also facilitated rubbing-over-the-wings. The form of this movement is such that most of the plumage on the crown and cheek areas, rather than just the

TABLE 6.13 Mean number of preen-ventral (per 15 minute observation period).

| | | <u>preen-</u> <u>ventral</u> | <u>preen-</u> <u>ventral-L</u> | <u>preen-</u> <u>ventral-R</u> |
|-----------|------|---------------------------------|-----------------------------------|-----------------------------------|
| 1.breast | cntl | 3.25 | 1.38 | 1.88 |
| | expl | 1.75 | 0.87 | 0.87 |
| 2.belly | cntl | 4.88 | 1.88 | 3.00 |
| | expl | 3.13 | 1.63 | 1.50 |
| 3.o.wings | cntl | 4.13 | 1.50 | 2.63 |
| | expl | 5.50 | 2.00 | 3.50 |
| 4.crown | cntl | 2.63 | 1.50 | 1.13 |
| | expl | 1.25 | 0.62 | 0.62 |
| 6.chin | cntl | 5.88 | 3.13 | 2.75 |
| | expl | 5.13 | 2.38 | 2.75 |
| 7.u.wings | cntl | 6.25 | 2.63 | 3.63 |
| | expl | 3.75 | 1.88 | 1.88 |
| 8.flanks | cntl | 6.50 | 2.00 | 4.50 |
| | expl | 2.75+ | 1.50 | 1.25+ |
| | | <u>all</u> | <u>trmt.side</u> | <u>non-trmt.side</u> |
| 5.cheek | cntl | 3.50 | 2.50 | 1.00 |
| | expl | 5.75 | 3.25 | 2.50 |

+ : $p \leq 0.05$ (two tailed)

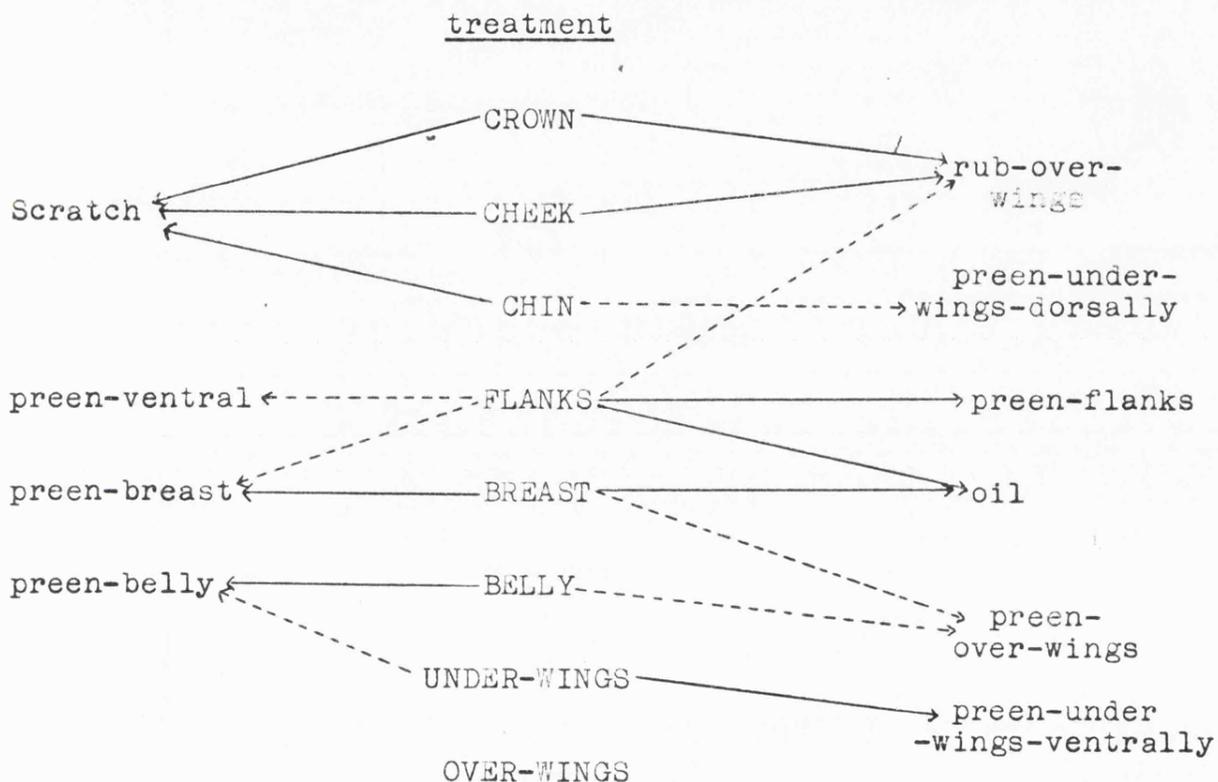
TABLE 6.14 Mean numbers of preen-breast and preen-belly
(per 15 minute observation period).

| <u>experiment</u> | | <u>preen-breast</u> | <u>preen-belly</u> |
|-------------------|------|---------------------|--------------------|
| 1.breast | cntl | 5.38 | 7.50 ⁺ |
| | expl | 93.37*** | 6.00 |
| 2.belly | cntl | 3.75 | 5.38 |
| | expl | 6.38 | 114.12*** |
| 3.o.wings | cntl | 3.75 | 4.25 |
| | expl | 2.50 | 4.13 |
| 4.crown | cntl | 4.13 | 2.50 |
| | expl | 7.63 | 3.87 |
| 5.cheek | cntl | 5.50 | 5.88 |
| | expl | 9.38 | 7.50 |
| 6.chin | cntl | 5.50 | 6.75 |
| | expl | 9.00 | 5.75 |
| 7.u.wings | cntl | 10.75 | 7.75 |
| | expl | 3.63 | 1.50+ |
| 8.flanks | cntl | 12.88 | 7.25 |
| | expl | 3.37+ | 4.25 |

*** : $p \leq 0.005$ (one tailed)

+ : $p \leq 0.05$ (two tailed)

FIGURE 6B Relationships between experimental treatments and the frequencies of preening movements. Solid line indicates a facilitatory relationship, broken line an inhibitory one.



note: preening movements were not recorded during experiments 9 & 10 dealing with the ventral area (see text).

area around the eye, would be rubbed against the dorsal surface of the body. This is important in view of Simmons' (1961) suggestion that there is a special shoulder-rubbing movement for cleaning the eye. Such movements may well have been included in the category rubbing-over-the-wings-dorsally, but only as a small minority.

Thus it would seem that wetting the head elicited two kinds of movement, scratching the head feathers with the foot and rubbing them elsewhere on the plumage. The foot is perhaps a less versatile instrument for preening than the bill, particularly when there is a need to smooth or squeeze water from the feathers. What peripheral stimuli, if any, elicit rubbing of areas of the plumage other than on the dorsal surface, must remain an open question. It is unfortunate that the preening/rubbing distinction could not easily be applied to other areas of the plumage. However, had treatment of the head areas facilitated, say, rubbing of the flanks, this would probably have shown up in the composite category preening plus rubbing of the flanks.

6.5 BATHING MOVEMENTS (Table 6.15)

6.5.1 Head-dips

Head-dips were significantly increased by treatment of the breast, over wings, crown, cheek, chin, flanks and under wing areas, that is, in all but the second experiment which involved treatment of the belly area. It thus seems that the general stimulus condition of wet plumage will elicit this component of bathing.

6.5.2 Wing-thrashing

Wing-thrashing was seen only in three birds which had been treated with detergent under the wings in experiment 7. Any facilitatory effect

TABLE 6.15 Mean numbers of head-dip and wing-thrash
(per 15 minute observation period).

| <u>experiment</u> | <u>head-dip</u> | <u>wing-thrash</u> |
|-------------------|-----------------|--------------------|
| 1.breast cntl | 25.63 | - |
| expl | 49.25* | - |
| 2.belly cntl | 25.63 | - |
| expl | 15.00 | - |
| 3.o.wings cntl | 27.38 | - |
| expl | 101.63*** | - |
| 4.crown cntl | 18.75 | - |
| expl | 41.13* | - |
| 5.cheek cntl | 19.00 | - |
| expl | 30.38* | - |
| 6.chin cntl | 21.50 | - |
| expl | 44.63* | - |
| 7.u.wings cntl | 26.00 | - |
| expl | 92.88*** | 1.63 |
| 8.flanks cntl | 15.13 | - |
| expl | 38.63* | - |
| 9.ventral cntl | 16.63 | - |
| expl | 30.63 | - |
| 10.ventral cntl | 9.88 | - |
| | 31.38*** | - |

* : $p \leq 0.05$ (one tailed)

*** : $p \leq 0.005$ (one tailed)

of this treatment came nowhere near statistical significance.

6.5.3 Bathing - general comments

Bouts of bathing usually begin with head-dipping, most often of low intensity at first, with a subsequent increase of vigour and intensity so as to incorporate tail-wagging and wing-shuffling. Bathing bouts that involve only head-dipping are usually of short duration whereas bouts that include wing-thrashing and/or somersaulting are usually fairly lengthy. This kind of observation led Weidmann (1956) to postulate a model for the control of these three bathing movements similar to Iersel and Bol's model for the control of preening: early in the bout the bathing drive is low and only head-dipping is activated; as the drive level increases, wing-thrashing and eventually somersaulting are produced. In short bouts, the drive never gets high enough for the latter two movements to be activated. There is no doubt that the form and patterning of bathing bouts suggest this kind of causal mechanism, but direct evidence is harder to come by.

The data clearly demonstrate that head-dips are facilitated by wetting many different areas of the plumage. However, the results show neither that wing-thrashing or somersaulting are facilitated by many treatments, nor that they are facilitated by particular treatments. There is thus little empirical evidence from the experiments from which to evaluate the differential threshold model as applied to bathing.

FIGURE 6C Mean number of occurrences of movements (per 15 minute observation period) in experiment 1 : control versus treatment of breast area.

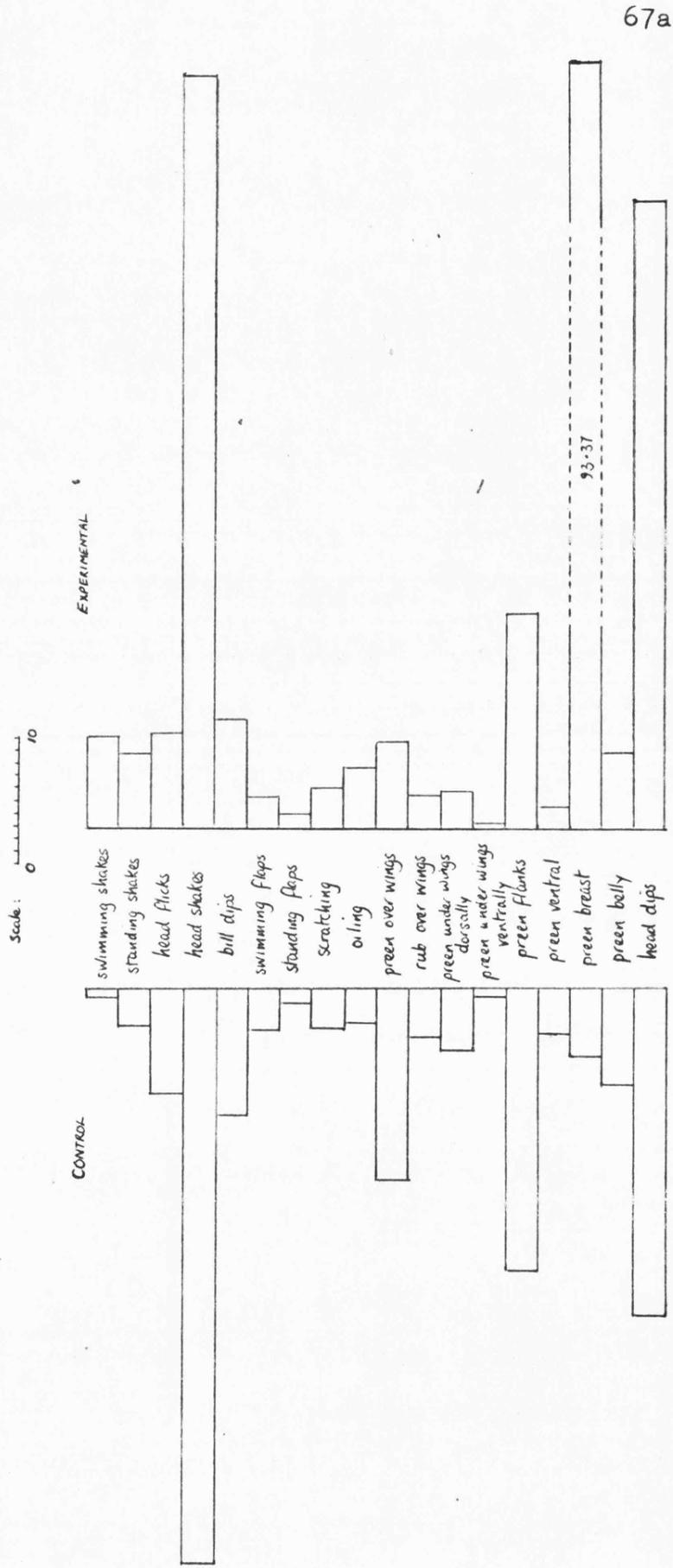


FIGURE 6D Mean number of occurrences of movements (per 15 minute observation period) in experiment 2 : control versus treatment of belly area.

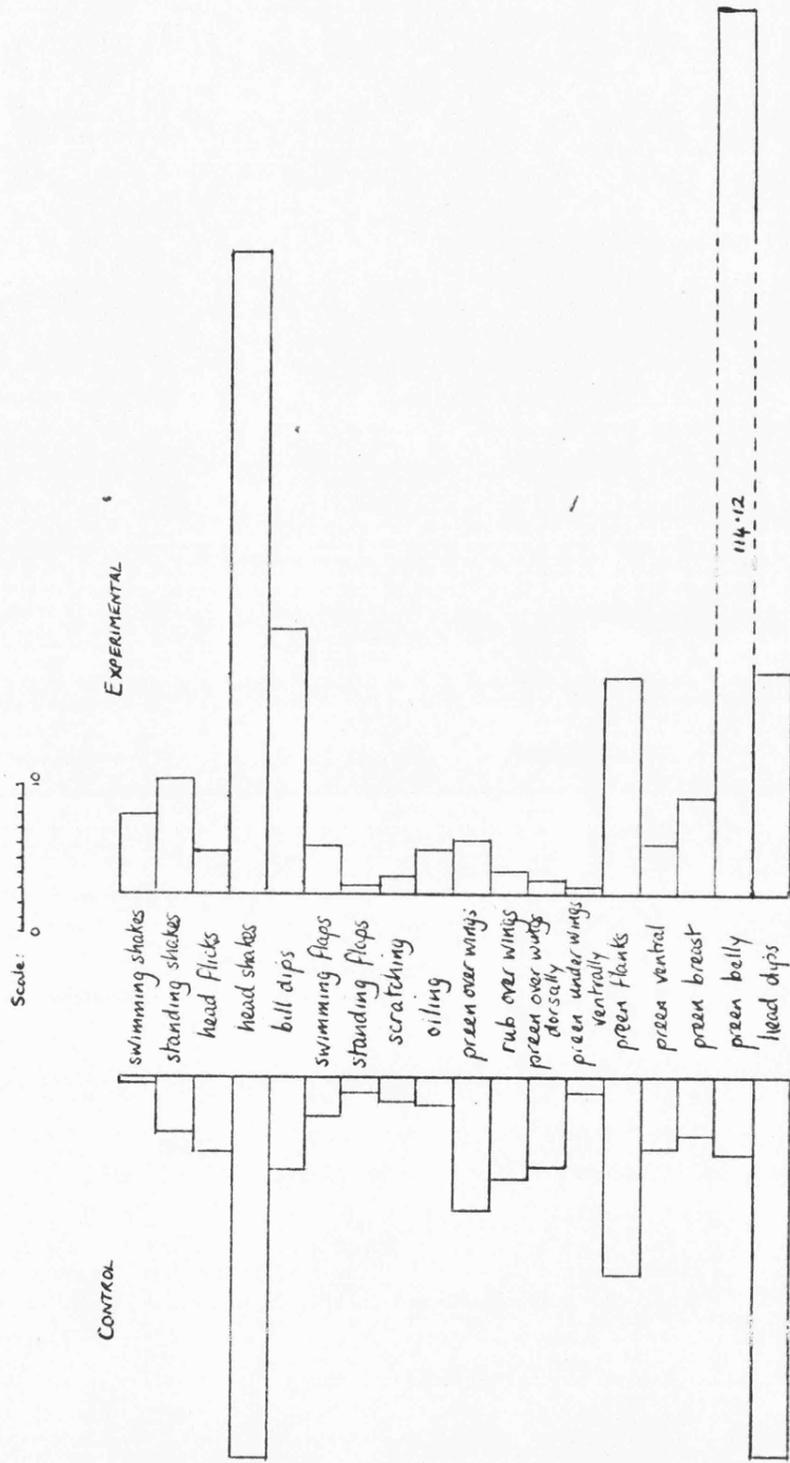


FIGURE 6E Mean number of movements (per 15 minute observation period) in experiment 3 : control versus treatment over the wings.

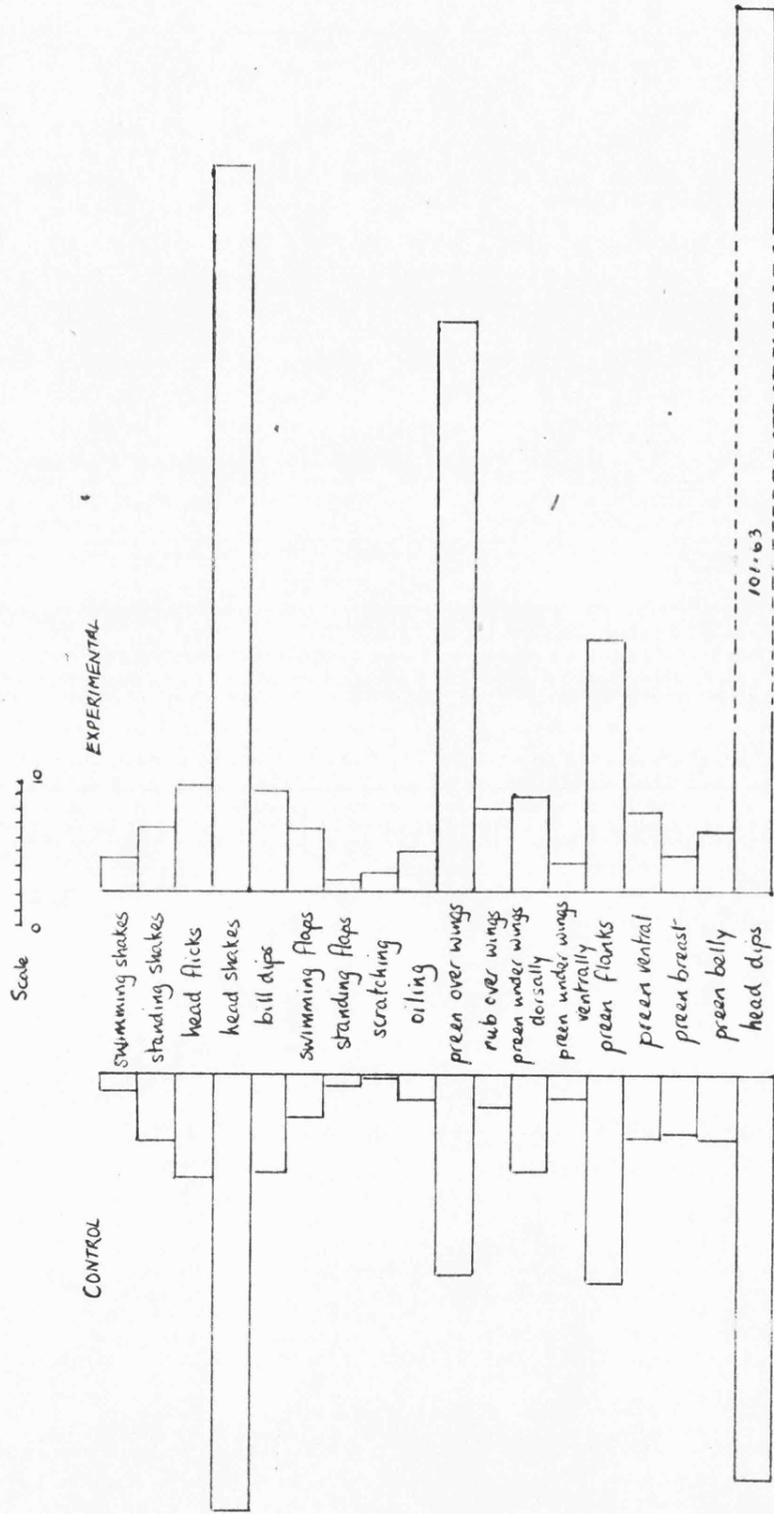


FIGURE 6F Mean number of movements (per 15 minute observation period)
in experiment 4 : control versus treatment of crown area.

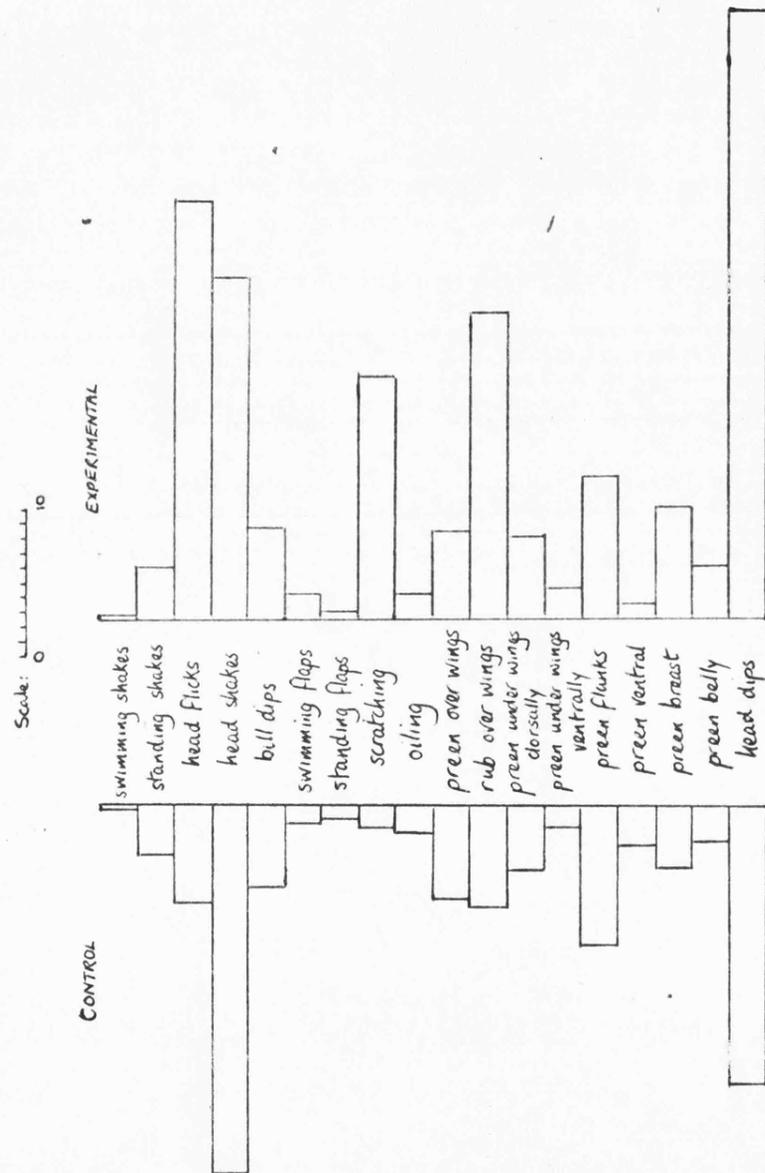


FIGURE 6G Mean number of occurrences of movements (per 15 minute observation period) in experiment 5 : control versus treatment of cheek area.

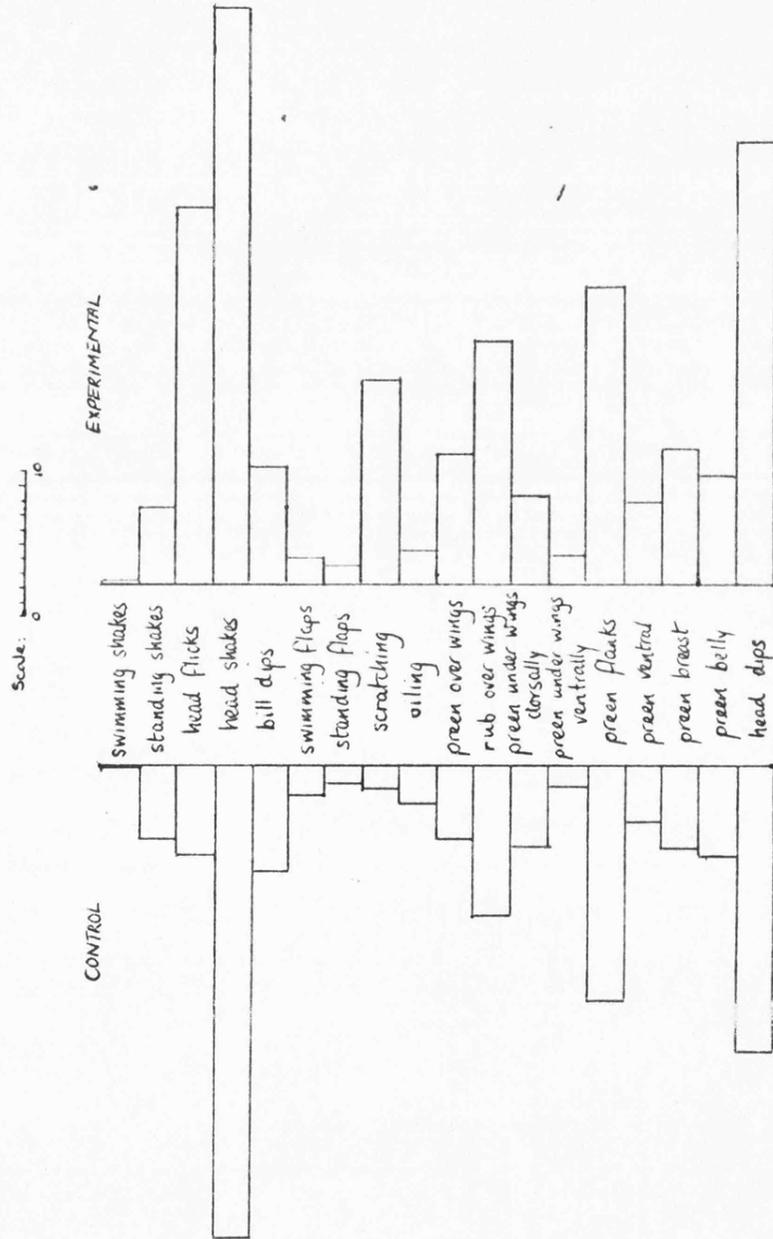


FIGURE 6H Mean number of occurrences of movements (per 15 minute observation period) in experiment 6 : control versus treatment of chin area.

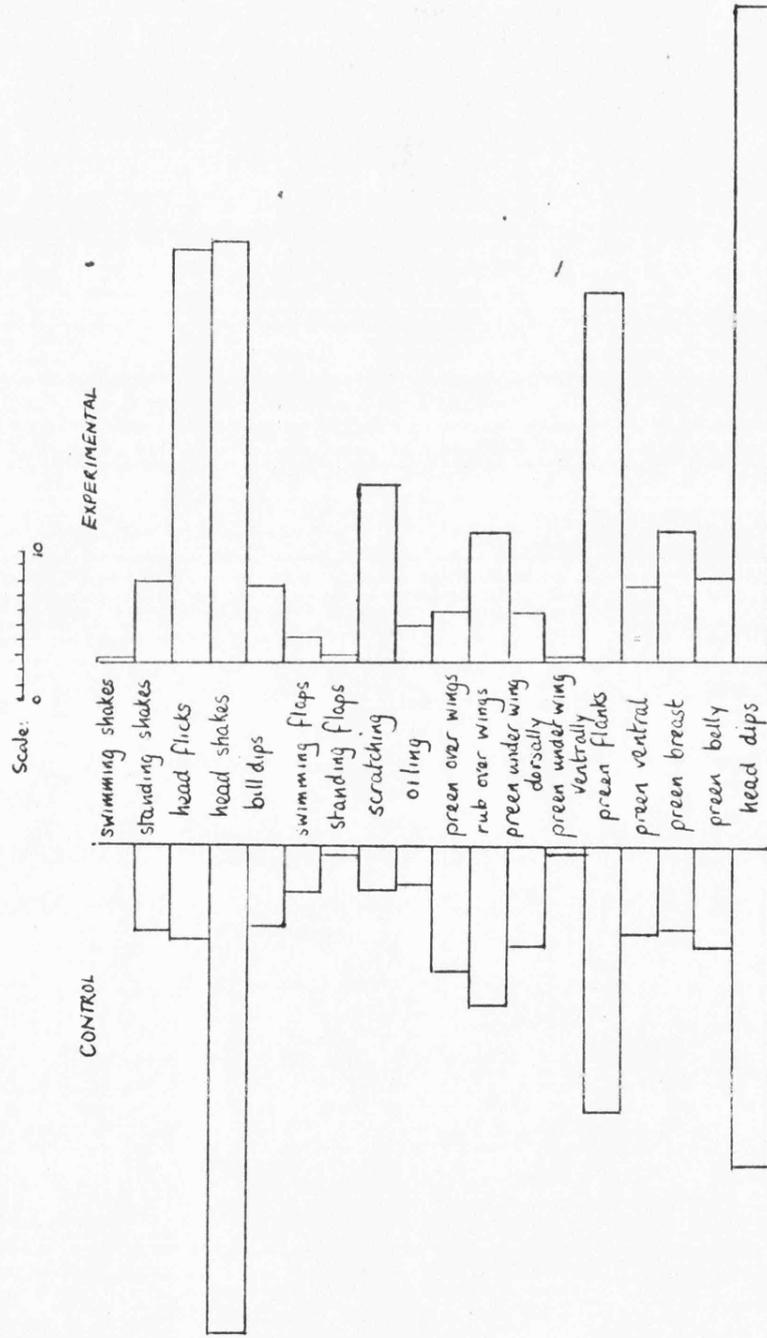


FIGURE 6J Mean number of occurrences of movements (per 15 minute observation period)
in experiment 7 : control versus treatment under the wings.

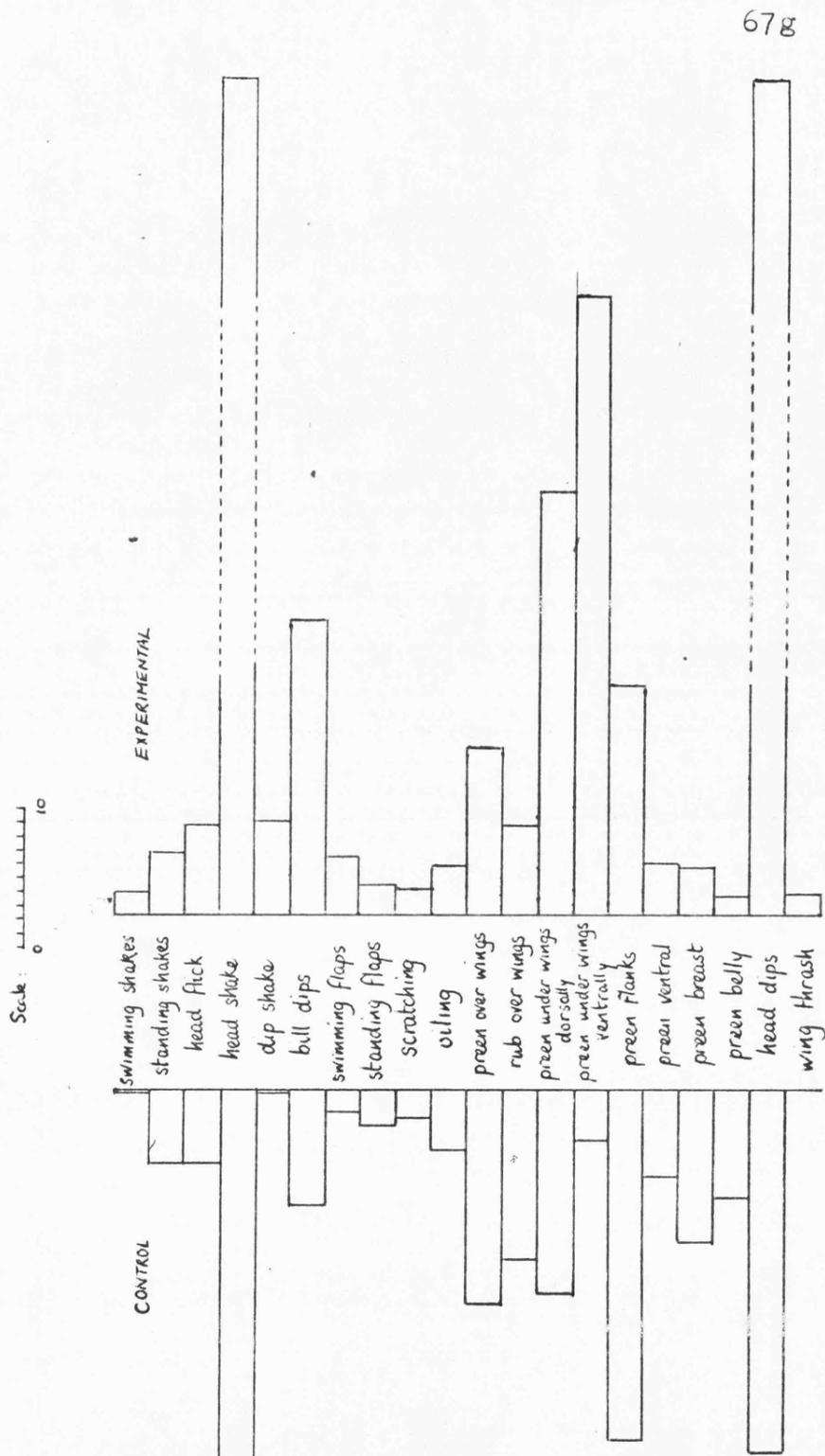


FIGURE 6K Mean number of occurrences of movements (per 15 minute observation period)
in experiment 8 : control versus treatment of flanks.

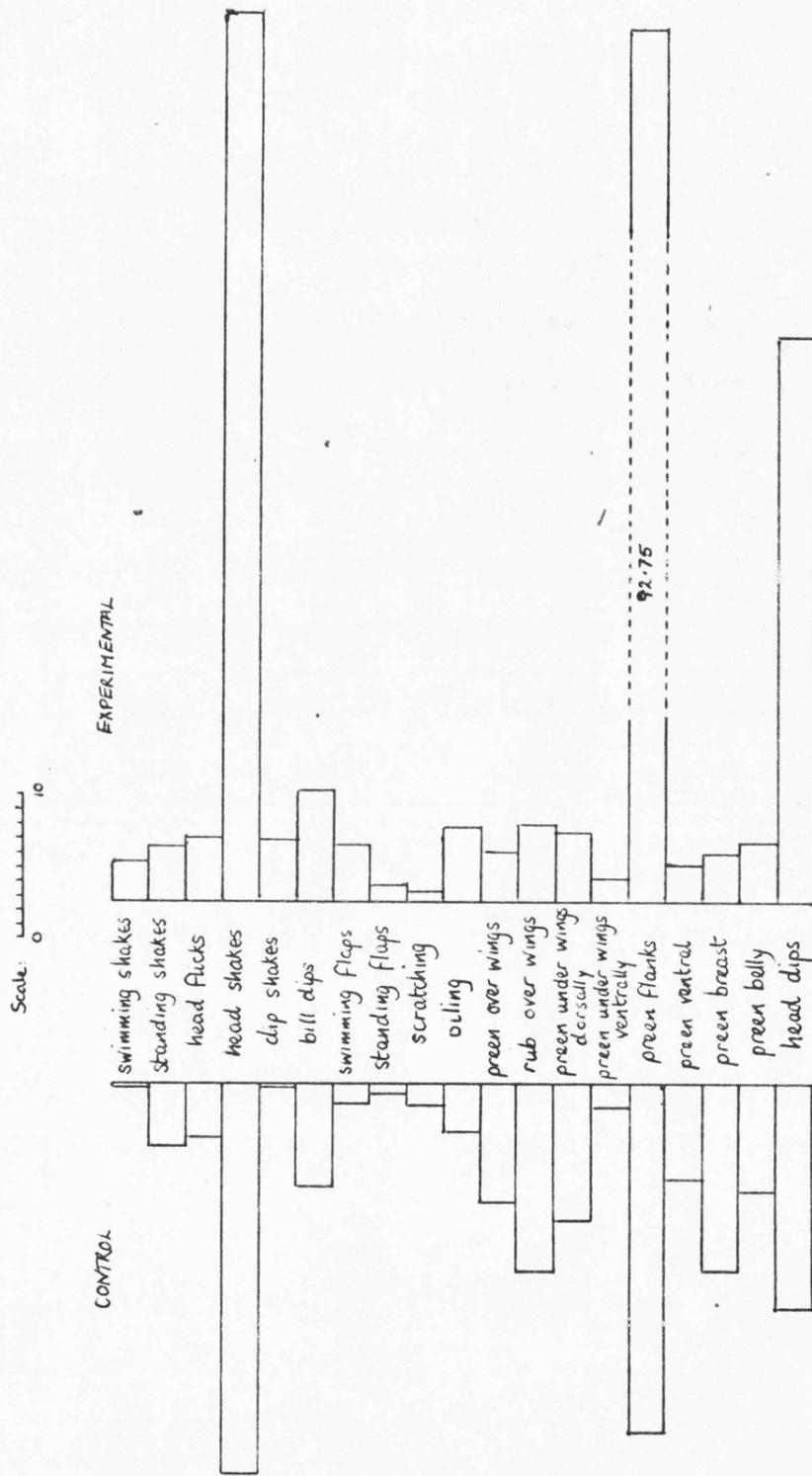


FIGURE 6L Mean number of occurrences of movements (per 15 minute observation period)
in experiment 9 : control versus treatment of ventral area.

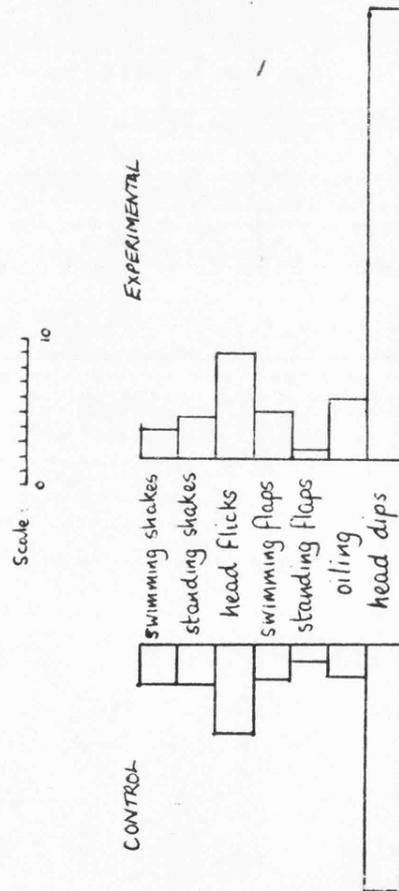
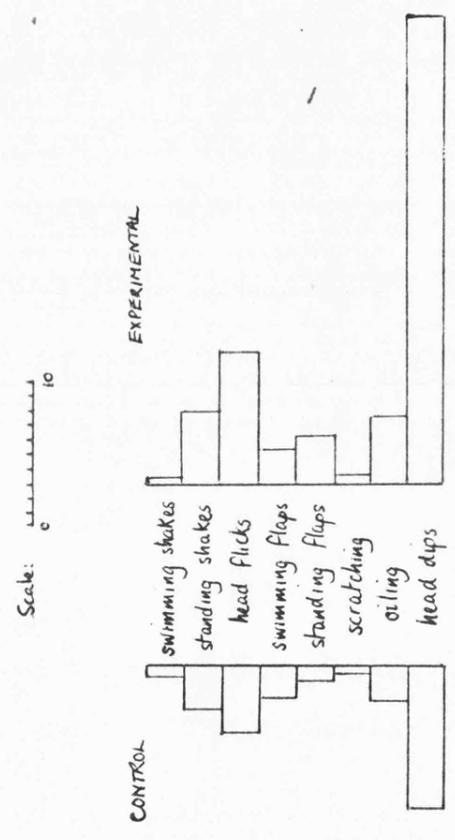


FIGURE 6M Mean number of occurrences of movements (per 15 minute observation period)
in experiment 10 : control versus treatment of ventral area.



CHAPTER SEVEN

RESULTS 2 : SEQUENCE ANALYSIS

7.1 INTRODUCTION

Measures of "amount" - frequency or durations of certain acts over a period of time - are the most easily handled descriptive statistics that can be applied to behaviour. Treated as interval or ordinal variables, such measures are well suited to conventional statistical procedures and hence to experimental analysis. Yet measures of amount are poor descriptors of many aspects of behaviour. Often, the functional significance of a set of activities is realised in its sequencing and patterning in time more adequately than in the frequency or duration of each activity. The success of a fighting animal is more likely to depend on the timing of blows rather than their sheer number. And the success of a blow may depend on whether it follows the right kind of lunge and how it is itself followed up. Success in sexual relations is dependent upon being able to copulate at the right point in a sequence of epigamic behaviour. The function of anti-predator mobbing displays depends on correctly timing the switches between approach and flight. And even with activities that are minimally related in terms of function, an animal has a very general time sharing task in allotting portions of the total time available to the different types of behaviour in his repertoire (McFarland 1974). Thus a major constraint on the organisation of behaviour is that of serial order (Lashley 1951).

Traditionally ethology, more than comparative psychology, has recognised the crucial importance of the problems of timing and sequencing for the understanding of behaviour. Empirical work on the subject derived impetus from an interest in causal (motivational) analysis although, to a degree, the rationale for this lies on functional grounds - the notion that functionally related activities, for instance the various components of a courtship sequence, are aggregated together in

time by virtue of their sharing common causal factors (Hinde 1970). Such considerations led to the development of methodologies for studying the sequential and temporal organisation of behaviour. Many of the methods devised are reviewed by Slater (1973).

7.1.1 Transition analysis

One class of method that has been used rather widely as a first step in the description of behaviour sequences is transition analysis. The simplest form that this can take is an examination of the frequency with which different activities occur in immediate succession in a sequence. To illustrate, if there are three activities, A, B and C, which occur in the sequence

A B A A C B A C B A C B

the couplets BA, AC and CB occur three times each, AA and AB once, and the other four couplets not at all. In all, there are eleven overlapping couplets in a sequence of twelve actions. Such data are normally cast into a transition matrix in which each couplet is cross-classified according to the first and second activity in that couplet:

| | | <u>second activity</u> | | | |
|-----------------|-------|------------------------|---|---|-------|
| | | A | B | C | total |
| | A | 1 | 1 | 3 | 5 |
| <u>first</u> | B | 3 | 0 | 0 | 3 |
| <u>activity</u> | C | 0 | 3 | 0 | 3 |
| | total | 4 | 4 | 3 | 11 |

Under the null hypothesis of a random ordering of A's, B's and C's, taking into account that the frequencies of the three activities differ from one another, the maximum likelihood expectation for the frequency of a given couplet can be calculated conveniently as the product of the

relevant row and column totals divided by the grand total. Thus, the expected frequency of the couplet AC is

$$\frac{\text{row 'A' total} \times \text{column 'C' total}}{\text{grand total}} = \frac{5 \times 3}{11} = 1.35$$

Clearly, when data in a transition matrix are derived from overlapping couplets, each action excepting the first and the last occurs once as the first member of a couplet, and once as a second. It follows that, apart from the "end effects", the row total for a given activity must equal the column total for the same activity. For activities occurring at the beginning and at the end of the sequence, the two marginal totals must differ by no more than one. In a relatively long sequence, this difference of one will be trivial compared with the total number of observations. It follows that the expected frequency for a given couplet of two different activities will be more or less the same as the expected frequency of the couplet in which the same two activities occur in the reverse order. This means that an uncomplicated comparison between the two observed frequencies will reveal whether two activities are linked asymmetrically - that is, are the activities (say) A and B linked more frequently as AB or as BA (Blurton Jones 1968)? This is conveniently referred to as symmetry analysis. Clearly it is not applicable to transitions on the descending diagonal of a transition matrix where the same rather than different movements occur in succession. Symmetry analysis is interesting' descriptively and, moreover, a positive result implies that the temporal association between two asymmetrically linked activities cannot be ascribed solely to their sharing common causal factors.

Transition analysis can be extended beyond the examination of couplets, to triplets, quadruplets and so on (Altmann 1965). In practice, this is seldom done as, if every possible triplet, quadruplet etc. is examined, the transition matrix becomes so large that, with a feasible

amount of data, many cells remain empty. More practically, and more usefully, transition analysis can be extended to alternate movements in a sequence.

Letting X stand for "any of the activities A, B or C", in the hypothetical data given above, the triplet AXB occurs three times, BXC and CXA occur twice, and AXA, BXA and AXC once. These data can also be cast into a 3 x 3 transition matrix by cross-classifying the triplets according to the first and third activities:

| | | <u>third activity</u> | | | |
|-----------------------|---|-----------------------|---|---|-------|
| | | A | B | C | total |
| <u>first activity</u> | A | 1 | 3 | 1 | 5 |
| | B | 1 | 0 | 2 | 3 |
| | C | 2 | 0 | 0 | 2 |
| total | | 4 | 3 | 3 | 10 |

The observed frequencies of these transitions between alternate movements can be compared with the frequencies expected under the null hypothesis of random ordering, and they can also be examined for symmetry.

Although it was not done in the present study, one can also ask whether the frequencies of transition between alternate movements deviate from what would be expected given the one-step dependency revealed by a matrix of transitions between adjacent movements. Most conveniently, matrices of conditional probabilities are calculated by dividing each cell frequency by its row total. Squaring (in the matrix algebra sense) the probability matrix for transitions between adjacent movements yields an expected matrix of probabilities for transitions between alternate movements (Jaffe and Feldstein 1970). Thus two-step sequential dependencies can be examined without the need to enumerate every possible triplet of activities.

Descriptively, the main advantage of the analysis between alternate movements is that it can reveal sequential linkages which could otherwise be hidden by the presence, in the data, of intervening "nuisance" activities. This reduces, to some extent, the dependence of transition analysis on just what behavioural categories are included or excluded from the repertoire to be analysed. It does not, of course, reduce the dependence of the results on the degree of lumping and splitting in the categories.

In contrast to the analysis reported in chapter 6, the main reason for applying sequential analysis to the behaviour of the experimental animals was descriptive, one reason being the analytical problems involved in testing the effects of an experimental factor on the sequential organisation of behaviour given that, as we have seen, the base rates of the various activities change in themselves. In principle one could compare, across the experimental conditions, measures of association calculated either for the matrices as a whole or for selected fourfold tables obtained by collapsing the full table around the cell for a particular transition. However, no known measure of association is robust enough, in the sense of being relatively resistant to the effects of varying marginal totals, to be applied realistically to the sparse matrices generated by the present data.

In comparing the frequency of particular transitions with the frequency expected under a random model, the analysis focuses on linkages which are noteworthy because of their frequent occurrence. It is to some degree arbitrary to ignore the potential information in transitions which occur rarely. However, the decision to do so is in keeping with the emphasis on description. Description in everyday experience most often focuses on phenomena noteworthy for their presence rather than on

those noteworthy for their absence. And in the present case, the neglect of rare events can be commended on the grounds that it brings into manageable proportions the task of presenting, in a digestible form, a mass of information about the sequential organisation of the animals' behaviour.

7.2 PROCEDURES

The set of activities considered in the transition analysis comprises all those activities recorded in experiments 1-8, as set out in chapters 5 and 6. In this set, standing and swimming versions of body-shake and wing-flap were distinguished, as were movements of preening a particular area of the plumage on left and right sides of the body. This rule was modified in the rather special case of the data from experiment 5 which involved the application of control and experimental treatments to the cheek area on one side of the head. Here, for both control and experimental conditions, preening movements were distinguished according to the dichotomy of treated side/untreated side rather than the left/right dichotomy. This follows the strategy employed for the presentation of the results in chapter 6.

Whilst it is not a prime concern of the transition analysis to examine the effects of the experimental versus control treatments, it is desirable to keep the two sets of data separate. Thus, each experiment yields two corpora of data, one for each treatment. Hence, from experiments 1-8, there are sixteen corpora of data, the data from experiments 9 and 10 being insufficiently detailed for meaningful analysis.

There remains the problem of how to combine data from the different subjects within any one corpus of data. Considerations that are familiar

in the context of contingency table analysis argue strongly against the simple pooling of data (Fleiss 1973). A simple alternative was adopted here. In each corpus of data, separate transition matrices were compiled for each subject. Sign tests across all subjects represented in a corpus were then used to make comparisons between observed and expected frequencies, and between the frequency of a given transition and its reverse in the symmetry analyses. Nominally, the criterion for rejection of the null hypotheses was the conventional $p = 0.05$ (one-tailed). With the large number of comparisons made, this has little meaning in terms of the type I error rate. It should be understood that the statistical test was used only as a screening device. Two transition matrices were compiled from each subject's data in a given corpus of data, one for transitions between adjacent movements and the other for transitions between alternate actions.

It has become common to eliminate from analyses transitions wherein a given movement is followed by itself. Such transitions lie on the main (descending) diagonal of the transition matrix. When they are eliminated from consideration, the expected frequencies for off-diagonal cells, containing transitions between different movements, must be adjusted using an iterative proportional fitting technique (Goodman 1968) or approximations (Lemon and Chatfield 1971). The reason for eliminating transitions on the diagonal is that, when the units of behaviour are defined so as to allow the same unit to occur in succession, transitions where a unit follows itself are commonly found to be very numerous indeed. The resulting high frequencies in the diagonal cells in the transition matrix may then obscure less powerful but more interesting relationships in off-diagonal cells. In the present study the diagonal cells were not eliminated because the units of behaviour were such that the occurrence of the same act in runs was neither

impossible nor common enough to swamp transitions between different movements. As we shall see, the results support the reasonableness of this course of action.

Finally, there is the problem of "pauses" in the stream of behaviour. In both types of transition analysis, between adjacent and alternate movements, transitions wherein two movements were separated by one or more empty ten second time intervals, were not counted. Inevitably, there were more transitions between alternative movements excluded on these grounds. Strictly speaking, exclusions such as these increase the problem of "end effects" mentioned in the previous section in connection with the symmetry analyses. Examination of the data, however, suggests that pauses are not particularly likely to be bounded by particular movements and so the influence of "end effects" is still minimal. The advantages of discounting transitions occurring over a pause are fairly obvious. Sequential linkages with an appreciable lag are certainly deleted or given less weight in the non-numerical awareness of order in everyday experience. In addition, whatever mechanisms underlie linkages between successive movements, they presumably decay over time.

7.3 RESULTS

In this section, we will examine those transitions revealed as being particularly noteworthy, in at least one corpus of data, by the screening procedures based on the symmetry analyses and on comparisons between observed and expected frequencies as applied to transitions between both adjacent and alternate movements. Naturally, transitions featuring in several corpora of data are of most interest.

To facilitate the integration of findings, the results of the transition analysis will be presented in sections with, as far as

possible, each section covering a group of transitions involving the same kind of movement. This is not quite as straightforward as in the previous chapter, and the sections follow a somewhat different order. First though, it is useful to present some of the main features of the results.

7.3.1 Overview

The screening procedures revealed as noteworthy: a total of 79 different transitions between adjacent movements and 54 different transitions between alternate ones. More alternate transitions were excluded from the analysis according to the pause criterion described above, and this doubtless contributes to the difference. Nonetheless, it is likely that there really is more sequential constraint between adjacent movements than between alternate ones.

The transitions revealed by the screening procedures involved almost all of the movements recorded. The most important exception was standing-flap. The others were dip-shake, which was recorded as a distinct movement only in experiments 7 and 8, and wing-thrash which only occurred in experiments 7 and 8.

The four movements swimming-flap, preen-ventral-left, preen-ventral-right and fly were noteworthy in transitions between adjacent movements but not between alternate ones.

Table 7.1 shows that more transitions were revealed in the corpora of data derived from the treatment conditions of the eight experiments than from the control conditions. This must reflect the greater overall amount of activity in the treatment conditions. Whether the behaviour was also more organised under the treatment condition is, as previously explained, impossible to tell.

TABLE 7.1 Number of different transitions revealed by screening procedures.

| <u>experiment</u> | <u>comparison with chance</u> | | <u>symmetry analysis</u> | |
|---|-------------------------------|----------------|--------------------------|----------------|
| | <u>control</u> | <u>exp'tal</u> | <u>control</u> | <u>exp'tal</u> |
| A. Transitions between adjacent movements | | | | |
| 1 | 4 | 9 | 4 | 15 |
| 2 | 4 | 7 | 4 | 9 |
| 3 | 5 | 5 | 6 | 8 |
| 4 | 4 | 5 | 3 | 5 |
| 5 | 7 | 8 | 6 | 12 |
| 6 | 8 | 11 | 9 | 11 |
| 7 | 7 | 12 | 14 | 24 |
| 8 | 5 | 9 | 6 | 10 |
| mean | 5.5 | 8.25 | 6.5 | 11.75 |
| B. Transitions between alternate movements | | | | |
| 1 | 2 | 9 | 3 | 4 |
| 2 | 3 | 3 | 2 | 9 |
| 3 | 2 | 3 | 2 | 1 |
| 4 | 1 | 2 | 0 | 3 |
| 5 | 2 | 7 | 1 | 7 |
| 6 | 3 | 4 | 3 | 6 |
| 7 | 3 | 6 | 3 | 8 |
| 8 | 6 | 3 | 3 | 8 |
| mean | 2.75 | 4.625 | 2.125 | 5.75 |

7.3.2 Transitions involving only shaking movements (Table 7.2)

Of the possible transitions involving only shaking movements, two were particularly prominent. These were swimming-flap to head-flick and bill-dip to head-shake, both of which were recognised by Weidmann (1956) and McKinney in their non-quantitative descriptive accounts.

In both control and treatment conditions of the majority of experiments, the transition swimming-flap to head-flick was more frequent than chance and more frequent than its converse. Nowhere did it feature as a significant transition between non-adjacent movements.

The transition bill-dip to head-shake was more frequent than chance, and more frequent than its converse, in the control and treatment conditions of a number of experiments. There is some evidence that this linkage holds for transitions between alternate movements as well as between adjacent ones. This probably reflects a tendency for bill-dips to be followed by two successive head-shakes. The only corpus of data from which the transition head-shake to head-shake was detected (flanks experiment, treatment condition) was also one of the three corpora to reveal the bill-dip to head-shake transition between alternate movements. The coding of dip-shake as an alternative category to some instances of bill-dip followed by head-shake, in the "under wings" and "flanks" experiments, did not seem to reduce markedly the prominence of the bill-dip to head-shake transition.

Other transitions between shaking movements were detected in single corpora of data only.

7.3.3 Transitions between pairs of preening movements (Table 7.3)

Rather few pairs of preening movements yielded more than isolated

TABLE 7.2 Corpora of data where screening procedures revealed transitions between shaking movements.

A. Transitions between adjacent movements.

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|---------------------------------|-------------------|---|------------------------------------|
| swimming-flap to head-flick | 1. breast | cntl & expl | cntl & expl |
| | 2. belly | expl | cntl & expl |
| | 3. ov. wings | cntl & expl | cntl & expl |
| | 4. crown | cntl & expl | cntl & expl |
| | 5. cheek | cntl | cntl & expl |
| | 6. chin | cntl & expl | cntl & expl |
| | 7. u. wings | expl | expl |
| | 8. flanks | - | expl |
| bill-dip to head-shake | 1. breast | expl | cntl & expl |
| | 2. belly | cntl & expl | cntl & expl |
| | 3. ov.wings | - | cntl |
| | 4. crown | - | expl |
| | 5. cheek | - | cntl |
| | 6. chin | expl | cntl |
| | 7. u.wings | expl | cntl & expl |
| | 8. flanks | expl | cntl & expl |
| head-flick to head-shake | 7. u.wings | - | expl |
| standing-shake to head-shake | 7. u.wings | expl | expl |
| head-shake to head-shake | 4. crown | cntl | N/A |

B. Transitions between alternate movements

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|-------------------|-------------------|---|------------------------------------|
| bill-dip to | 1. breast | cntl | - |
| head-shake | 4. crown | - | expl |
| | 8. flanks | cntl | - |
| head-shake to | | | |
| standing-shake | 2. belly | - | expl |
| head-flick to | | | |
| standing-shake | 8. flanks | - | expl |
| head-shake to | | | |
| head-flick | 6. chin | - | cntl |
| head-flick to | | | |
| head-shake | 2. belly | - | expl |
| head-flick to | | | |
| head-flick | 5. cheek | expl | N/A |
| | 6. chin | expl | N/A |

noteworthy transitions. Most consistent were the transitions preen-flank-left to preen-ventral-left and preen-flank-right to preen-ventral-right. These linkages were found in both control and treatment conditions of several experiments, but never for alternate movements. One of the converse linkages, preen-ventral-right to preen-flank-right was detected from a single corpus.

For many of the other transitions too, the corresponding "mirror image" transition, involving the same two movements directed toward the other side of the body, was also detected. Examples are: rub-over-wing (left or right) to preen-flank (left or right) and preen breast to preen-flank (left or right).

Two transitions, both between alternate movements, involve crossing over from one side of the body to the other. These were preen-flank-left to oil-right and preen-flank-right to preen-flank-left. Such crossover transitions featured nowhere among adjacent transitions. This confirms the impression that the birds tended to deal with several areas on one side of the body before changing to the other side.

There was some indication that homogenous sequences, involving a transition from one movement to itself, were more frequent when there was an intervening movement, that is, between alternate movements. As we shall see in the next section, head-shake was probably the most frequent intermediate movement.

7.3.4 Transitions between head-shake and preening movements (Table 7.4)

Noticeable for its absence is any type of sequential linkage between head-shaking and scratching.

Of the remaining sixteen preening movements (including seven pairs

TABLE 7.3 Corpora of data where screening procedures revealed transitions between preening movements.

A. Transitions between adjacent movements

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> | <u>symmetry</u> |
|--------------------|-------------------|--------------------|-----------------|
| | | <u>with chance</u> | <u>analysis</u> |
| preen-flank-R to | 3. ov.wings | cntl | expl |
| preen-ventral-R | 6. chin | cntl & expl | - |
| | 7. u.wings | cntl & expl | cntl & expl |
| preen-flank-L to | 3. ov.wings | expl | expl |
| preen-ventral-L | 6. chin | expl | - |
| | 7. u.wings | - | cntl |
| | 8. flanks | cntl & expl | cntl |
| rub-ov.wing-L to | 6. chin | cntl | - |
| preen-flank-L | 7. u.wings | cntl | cntl |
| rub-ov.wing-R to | | | |
| preen-flank-R | 7. u.wings | - | cntl |
| preen-breast to | | | |
| preen-flank-L | 6 chin | expl | expl |
| preen-flank-L to | | | |
| preen-breast | 1. breast | - | expl |
| preen-breast to | | | |
| preen-flank-R | 7. u.wings | cntl | - |
| oil-R to | | | |
| preen-ov.wing-R | 7. u.wings | - | cntl |
| preen-ov.wing-R to | | | |
| preen-flank-R | 7. u.wings | - | cntl |
| preen-breast to | | | |
| preen-belly | 6. chin | cntl | - |
| preen-flank-L to | | | |
| preen-flank-L | 8. flanks | expl | N/A |
| preen-ventral-R to | | | |
| preen-flank-R | 6. chin | expl | - |

A. Transitions between adjacent movements (continued)

| <u>transition</u> | <u>experiment</u> | <u>comparison with chance</u> | <u>symmetry analysis</u> |
|--------------------------------|-------------------|-----------------------------------|------------------------------|
| preen-ov.wing-R to preen | | | |
| -u.wing-ventrally-R | 7. u.wings | expl | expl |
| preen-flank-L to | | | |
| preen-belly | 2. belly | - | expl |
| preen-flank(trmt side) to | | | |
| preen-ventrally(trmt side) | 5. cheek | cntl & expl | expl |
| preen-flank(non-trmt side) to | | | |
| preen-ventrally(non-trmt side) | " | - | expl |
| preen-ov.wing (trmt side) to | | | |
| preen-flank(trmt side) | " | - | expl |

B. Transitions between alternate movements

| | | | |
|-------------------------------|-----------|------|------|
| preen-flank-L to | | | |
| preen-flank-L | 8. flanks | expl | N/A |
| preen-flank(non-trmt side) to | | | |
| preen-flank(non-trmt side) | 5. cheek | cntl | N/A |
| preen-flank-R to | | | |
| preen-flank-L | 6. chin | expl | - |
| preen-breast to | | | |
| preen-belly | 1. breast | - | expl |
| preen-breast to | | | |
| oil-R | 1. breast | expl | - |
| preen-breast to | | | |
| oil(trmt side) | 5. cheek | expl | expl |
| preen-breast to | | | |
| oil-L | 1. breast | expl | - |
| oil-R to preen breast | 1. breast | expl | - |
| preen-breast to | | | |
| preen-breast | 1. breast | expl | N/A |

B. Transitions between alternate movements (continued)

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|--|-------------------|---|------------------------------------|
| preen-belly to preen belly | 2. belly | expl | N/A |
| preen-ov.wing-R to preen-flank-R | 7. u.wings | - | cntl |
| preen-ov.wing(trmt side) to preen-flank(trmt side)- oil-R to | 5. cheek | expl | / |
| preen-flank-R | 8. flanks | - | expl |
| preen-u.wing-dorsally-R to preen-flank-R | 7. u.wings | - | expl |
| preen-u.wing-ventrally-L to preen-flank-L | 7. u.wings | - | expl |
| preen-flank-L to oil-R | 8. flanks | - | expl |
| preen-breast to preen-flank-L | 8. flanks | cntl | - |

B. Transitions between alternate movements (continued)

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|--|-------------------|---|------------------------------------|
| preen-belly to preen belly | 2. belly | expl | N/A |
| preen-ov.wing-R to preen-flank-R | 7. u.wings | - | cntl |
| preen-ov.wing(trmt side) to preen-flank(trmt side)- | 5. cheek | expl | / |
| oil-R to preen-flank-R | 8. flanks | - | expl |
| preen-u.wing-dorsally-R to preen-flank-R | 7. u.wings | - | expl |
| preen-u.wing-ventrally-L to preen-flank-L | 7. u.wings | - | expl |
| preen-flank-L to oil-R | 8. flanks | - | expl |
| preen-breast to preen-flank-L | 8. flanks | cntl | - |

TABLE 7.4 Corpora of data where screening procedures revealed transitions head-shake and preening movements.

A. Transitions between adjacent movements.

| <u>transition</u> | <u>experiment</u> | <u>comparison of symmetry</u> | |
|----------------------------|-------------------|-------------------------------|-----------------|
| | | <u>with chance</u> | <u>analysis</u> |
| head-shake to | 1. breast | expl | expl |
| oil-L | 7. u.wings | cntl | cntl & expl |
| | 8. flanks | cntl & expl | cntl & expl |
| head-shake to | 6. chin | expl | expl |
| oil-R | 7. u.wings | - | cntl & expl |
| | 8. flanks | expl | expl |
| head-shake to | 1. breast | - | expl |
| preen-o.wing-R | 3. o.wings | - | expl |
| | 4. crown | cntl | cntl |
| head-shake to | 3. o.wings | - | expl |
| preen-o.wing-L | 4. crown | expl | - |
| | 7. u.wings | - | cntl & expl |
| head-shake to | | | |
| preen-owing(trmt side) | 5. cheek | - | expl |
| head-shake to | 3. o.wings | - | cntl |
| preen-uwing-dorsally-L | 6. chin | - | expl |
| | 7. u.wings | expl | cntl & expl |
| | 8. flanks | - | cntl |
| head-shake to preen-u.wing | | | |
| -dorsally (trmt side) | 5. cheek | cntl | cntl |
| head-shake to | 6. chin | | cntl |
| preen-u.wing-dorsally-R | 7. u.wings | | expl |
| head-shake to preen-u.wing | | | |
| -dorsally(non-trmt side) | 5. cheek | | expl |
| preen-belly to | | | |
| head-shake | 1. breast | cntl | - |

A. Transitions between adjacent movements (continued)

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|----------------------------|-------------------|---|------------------------------------|
| head-shake to | | | |
| preen-belly | 2. belly | expl | - |
| head-shake to | | | |
| preen-flank-L | 8. flanks | expl | - |
| head-shake to | | | |
| preen-flank-R | 1. breast | - / | cntl |
| | 7. u.wings | expl | - |
| | 8. flanks | - | cntl |
| preen-flank-L to | | | |
| head-shake | 1. breast | - | expl |
| head-shake to preen-u.wing | | | |
| -ventrally-R | 7. u.wings | expl | - |
| head-shake to preen-u.wing | | | |
| -ventrally-L | 7. u.wings | expl | expl |
| head-shake to | | | |
| preen-breast | 1. breast | expl | - |
| preen-ventral-R to | | | |
| head-shake | 7. u.wings | - | cntl |

B. Transitions between alternate movements

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|--------------------------|-------------------|---|------------------------------------|
| head-shake to | 2. belly | expl | expl |
| preen-ov.wing-R | 7. u.wings | cntl | - |
| head-shake to | 1. breast | - | cntl |
| preen-o.wing-L | 8. flanks | cntl | cntl |
| head-shake to preen- | 1. breast | - | cntl |
| u.wing-dorsally-L | 6. chin | - / | expl |
| | 7. u.wings | - | expl |
| head-shake to preen- | 2. belly | cntl | - |
| u.wing-dorsally-R | 7. u.wings | expl | - |
| | 8. flanks | cntl | cntl |
| preen-belly to | 1. breast | expl | expl |
| head-shake | 2. belly | expl | expl |
| | 3. o.wings | expl | - |
| head-shake to preen- | | | |
| u.wing-ventrally-R | 7. u.wings | expl | - |
| head-shake to preen- | | | |
| o.wing(non-trmt side) | 5. cheek | expl | - |
| preen-u.wing-ventrally-L | | | |
| to head-shake | 7. u.wings | expl | - |

of left/right versions of essentially the same movement), twelve showed a tendency to follow immediately after head-shake and six tended to occur as the next but one movement. In contrast, three types of preening movement exhibited a tendency to immediately precede head-shake and two tended to precede head-shake with an intervening movement.

7.3.5 Transitions involving preening movements and shaking movements other than head-shake (Table 7.5)

In marked contrast to the case with head-shake, the preening movement most consistently associated with head-flick was scratching. However, these linkages were not widespread beyond the treatment conditions of experiments involving stimulation of areas of the head. The transition head-flick to rub-over-wing (left or right) also appear in the corpora of data from the treatment condition of the crown and cheek areas. Stimulation of the head, it will be recalled, facilitated scratching and rubbing movements, as well as head-flicking.

Like head-shake, bill-dip was linked with a number of different preening movements, but seldom did each linkage occur in more than one corpus of data. In fact, these linkages occur only in the treatment conditions of experiments where stimulation was applied to the area involved in the preening component of the transition.

Of the other shaking movements, standing-shake was linked with preening of the breast and belly areas in a few corpora of data. As we have seen, these movements tend to be elicited by the same factors, but these linkages are not confined to data where experimental treatments facilitated standing-shakes or preening of the areas in question.

TABLE 7.5 Corpora of data where screening procedures revealed transitions between a preening movement and a shaking movement other than head-shake.

A. Transitions between adjacent movements.

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|---|----------------------|---|------------------------------------|
| head-flick to scratch (trmt side) | 5. cheek | expl | - |
| head-flick to scratch-R | 4. crown | expl | - |
| scratch-L to head-flick | 4. crown | expl | - |
| head-flick to rub-o.wing(trmt side) | 5. cheek | expl | - |
| head-flick to rub-o.wing-L | 4. crown | - | expl |
| head-flick to rub-o.wing-R | 4. crown | - | expl |
| standing-shake to preen-breast | 1. breast 6. chin | expl - | expl expl |
| standing-shake to preen-belly | 2. belly | expl | - |
| preen-belly to bill-dip | 2. belly | expl | expl |
| preen-breast to bill-dip | 1. breast | - | expl |
| preen-u.wing-dorsally-L to bill-dip | 7. u.wings | - | expl |
| preen-u.wing-ventrally-L to bill-dip | 7. u.wings | - | expl |

A. Transitions between adjacent movements(continued).

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|-----------------------------|-------------------|---|------------------------------------|
| preen-breast to | | | |
| standing-shake | 7. u.wings | - | cntl |
| preen-u.wing-ventrally-R to | | | |
| bill-dip | 7. u.wings | - | expl |
| preen-flank-L to | | | |
| bill-dip | 8. flanks | - / | expl |

B. Transitions between alternate movements.

| | | | |
|--------------------------|----------|------|------|
| scratch (trmt side) to | | | |
| head-flick | 5. cheek | expl | expl |
| scratch-L to | | | |
| head-flick | 6. chin | - | expl |
| scratch-R to | | | |
| head-flick | 4. crown | expl | - |
| standing-shake to | | | |
| preen-belly | 2. belly | - | expl |
| rub-o.wing(trmt side) to | | | |
| head-flick | 5. cheek | - | expl |

7.3.6 Transitions involving head-dip (Table 7.6)

The sequence head-dip to head-dip was the most frequent linkage involving this movement. It occurred in excess of chance, between both adjacent and alternate movements, in the majority of experiments.

The next most prominent linkage involving head-dip was the transition head-dip to swimming-flap which was more frequent than its converse, in both alternate and adjacent transitions, in the majority of experiments. As a transition between alternate movements, this linkage exceeded chance in the majority of experiments, but only once as a transition between adjacent movements. The reverse transition, swimming-flap to head-dip, exceeded its converse in a single corpus.

The linkage head-flick to head-dip, and its converse head-dip to head-flick, featured in a number of corpora of data. Under the treatment condition of the cheek experiment, head-dip to head-flick exceeded chance, exceeded its converse and its converse exceeded chance too. This suggests that, though asymmetrically linked, these two movements are particularly strongly associated together in time.

The symmetry analyses showed a number of preening movements as preceding head-dip. Such linkages featured particularly strongly under treatment conditions but varied greatly from experiment to experiment.

Overall, the findings accord well with the general impressions that (1) head-dips occur in bouts during which, often, one head-dip is followed immediately by another; (2) bouts tend to be terminated by wing-flapping; (3) within bouts, runs of head-dips are often broken by single head-flicks; (4) bouts of head-dips also include a variety of preening movements to produce sequences referred to by McKinney as "washing".

TABLE 7.6 Corpora of data where screening procedures revealed transitions involving head-dip.

A. Transitions between adjacent movements.

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|-------------------|-------------------|---|------------------------------------|
| head-dip to | 1. breast | cntl & expl | N/A |
| head-dip | 2. belly | cntl & expl | N/A |
| | 3. o.wings | cntl & expl | N/A |
| | 5. cheek | cntl | N/A |
| | 6. chin | cntl & expl | N/A |
| | 7. u.wings | cntl & expl | N/A |
| | 8. flanks | cntl & expl | N/A |
| head-dip to | | | |
| swimming-flap | 2. belly | cntl | cntl & expl |
| | 3. o.wings | - | cntl |
| | 5. cheek | - | cntl & expl |
| | 6. chin | - | cntl & expl |
| | 7. u.wings | - | expl |
| | 8. flanks | - | expl |
| head-dip to | | | |
| head-flick | 1. breast | expl | - |
| | 5. cheek | expl | expl |
| | 6. chin | expl | expl |
| head-flick to | | | |
| head-dip | 5. cheek | expl | |
| head-shake to | | | |
| head-dip | 2. belly | - | cntl |
| bill-dip to | | | |
| head-dip | 7. u.wings | - | expl |
| head-dip to | | | |
| head-shake | 6. chin | - | cntl |
| | 7. u.wings | - | expl |

TABLE 7.6 continued

A. Transitions between adjacent movements (continued).

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|-----------------------------|-------------------|---|------------------------------------|
| rub-o.wing.-L to | | | |
| head-dip | 4. crown | - | expl |
| rub-o.wing(trmt side) to | | | |
| head-dip | 5. cheek | - | expl |
| swimming-flap to | | | |
| head-dip | 1. breast | - | expl |
| swimming-shake to | | | |
| head-dip | 1. breast | - | expl |
| preen-breast to | | | |
| head-dip | 1. breast | - | expl |
| enter-water to | | | |
| head-dip | 2. belly | - | expl |
| preen-o.wing-L to | | | |
| head-dip | 3. o.wings | - | expl |
| scratch(trmt side) to | | | |
| head-dip | 5. cheek | - | expl |
| preen-u.wing-ventrally-R to | | | |
| head-dip | 7. u.wings | - | expl |
| preen-flank-L to | | | |
| head-dip | 8. flanks | - | expl |
| preen-u.wing-dorsally-L to | | | |
| head-dip | 7. u.wings | - | expl |
| preen-u.wing-dorsally-R to | | | |
| head-dip | 7. u.wings | - | expl |

B. Transitions between alternate movements.

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|-------------------|-------------------|---|------------------------------------|
| head-dip to | | | |
| head-dip | 1. breast | cntl & expl | N/A |
| | 2. belly | cntl | N/A |
| | 3. o.wings | cntl & expl | N/A |
| | 4. crown | cntl & expl | N/A |
| | 5. cheek | cntl & expl | N/A |
| | 6. chin | cntl & expl | N/A |
| | 7. u.wings | cntl & expl | N/A |
| | 8. flanks | cntl & expl | N/A |
| head-dip to | | | |
| swimming-flap | 1. breast | expl | cntl & expl |
| | 2. belly | cntl | cntl & expl |
| | 3. o.wings | cntl & expl | cntl & expl |
| | 4. crown | - | expl |
| | 5. cheek | - | cntl & expl |
| | 6. chin | cntl | cntl & expl |
| | 7. u.wings | cntl & expl | cntl & expl |
| | 8. flanks | cntl & expl | cntl & expl |
| head-dip to | | | |
| head-flick | 1. breast | expl | - |
| | 3. o.wings | - | cntl |
| | 8. flanks | - | expl |
| head-flick to | | | |
| head-dip | 5. cheek | expl | expl |
| | 6. chin | expl | - |
| head-shake to | | | |
| head-dip | 6. chin | - | expl |
| | 7. u.wings | - | cntl |

B. Transitions between alternate movements (continued).

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|-----------------------------|-------------------|---|------------------------------------|
| bill-dip to | | | |
| head-dip | 2. belly | - | cntl |
| enter-water to | | | |
| head-dip | 2. belly | - | expl |
| head-dip to | | | |
| scratch (trmt side) | 5. cheek | - / | expl |
| head-dip to | | | |
| scratch-R | 4. crown | - | expl |
| head-dip to | | | |
| rub-o.wing(trmt side) | 5. cheek | - | expl |
| drink to | | | |
| head-dip | 7. u.wings | - | expl |
| preen-u.wings-dorsally-L to | | | |
| head-dip | 7. u.wings | - | expl |
| preen-u.wing-ventrally-R to | | | |
| head-dip | 7. u.wings | - | expl |

7.3.7 Transitions between comfort movements and non-comfort movements (Table 7.7)

The linkage drink to head-shake was the most prominent of this group of transitions. Between adjacent movements, it exceeded chance in a majority of control conditions, and was more frequent than its converse in a majority of both control and treatment conditions. The converse sequence head-shake to drink was represented but weakly in the results, and then only in transitions between alternate movements. The sequence drink to head-shake is easily interpreted in terms of head-shaking being a response to water on the bill.

The linkage head-flick to leave-water featured as a significant transition in a number of cases. It was more marked than the linkage enter-water to head-flick. In this sense, head-flick occurs in the context of what McKinney called a "transitional situation", that is before a change in activity type.

The sequences leave-water to standing-shake, standing-shake to enter-water and swimming-shake to leave-water were all prominent. Of course, the converse of each of these transitions is logically impossible and thus, in the symmetry analyses, these particular findings are trivial.

7.3.8 Transitions between pairs of non-comfort movements (Table 7.8)

The linkage fly to enter-water exceeded chance level in both conditions of every experiment. This indicates that birds usually landed on the water rather than on land.

In several instances, the linkage enter-water to drink featured in the results. This sequence is readily noticed in unsystematic observations.

TABLE 7.7 Corpora of data where screening procedures revealed transitions between comfort movements and non-comfort movements.

A. Transitions between adjacent movements.

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|-------------------|-------------------|---|------------------------------------|
| drink to | | | |
| head-shake | 1. breast | - | cntl & expl |
| | 3. o.wings | expl | expl |
| | 5. cheek | expl | cntl & expl |
| | 6. chin | expl | cntl & expl |
| | 7. u.wings | cntl | cntl & expl |
| | 8. flanks | cntl | cntl & expl |
| leave-water to | | | |
| standing-shake | 1. breast | expl | expl |
| | 2. belly | - | expl |
| | 3. o.wings | cntl | cntl |
| | 6. chin | - | expl |
| | 8. flanks | - | expl |
| head-flick to | | | |
| leave-water | 3. o.wings | - | cntl & expl |
| | 5. cheek | expl | expl |
| | 6. chin | cntl | cntl & expl |
| | 7. u.wings | expl | expl |
| standing-shake to | | | |
| enter-water | 4. crown | - | cntl |
| | 5. cheek | - | cntl |
| | 6. chin | - | cntl |
| swimming-shake to | | | |
| leave-water | 1. breast | - | expl |
| | 2. belly | - | expl |

TABLE 7.7 continued

A. Transitions between adjacent movements (continued).

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|--------------------------------|-------------------|---|------------------------------------|
| enter-water to head-flick | 6. chin | - | expl |
| leave-water to head-shake | 7. u.wings | - | expl |
| preen-breast to enter-water | 1. breast | - / | expl |
| preen-belly to enter-water | 2. belly | - | expl |
| preen-flank-L to drink | 8. flanks | - | expl |

B. Transitions between alternate movements.

| | | | |
|---------------------------------|-------------|------|-------------|
| drink to head-shake | 6. chin | cntl | expl |
| head-shake to drink | 1. breast | expl | expl |
| swimming-flap to leave-water | 6. chin | - | cntl & expl |
| | 7. u. wings | expl | expl |
| | 8. flanks | - | expl |
| preen-belly to enter water | 2. belly | - | expl |
| leave-water to preen-flank-L | 8. flanks | - | expl |
| leave-water to preen-belly | 2. belly | - | expl |

TABLE 7.8 Corpora of data where screening procedures revealed transitions between non-comfort movements.

A. Transitions between adjacent movements.

| <u>transition</u> | <u>experiment</u> | <u>comparison</u> <u>with chance</u> | <u>symmetry</u> <u>analysis</u> |
|-------------------|-------------------|---|------------------------------------|
| fly to | | | |
| enter-water | 1. breast | cntl & expl | - |
| | 2. belly | cntl & expl | - |
| | 3. o.wings | cntl & expl | - |
| | 4. crown | cntl & expl | - |
| | 5. cheek | cntl & expl | - |
| | 6. chin | cntl & expl | - |
| | 7. u.wings | cntl & expl | - |
| | 8. flanks | cntl & expl | - |
| enter-water to | | | |
| drink | 5. cheek | cntl | - |
| | 6. chin | cntl | cntl |
| | 8. flanks | expl | - |
| enter-water to | | | |
| leave-water | 5. cheek | cntl | - |

B. Transitions between alternate movements.

| | | | |
|----------------|-----------|---|------|
| enter-water to | | | |
| drink | 8. flanks | - | expl |

7.4 DISCUSSION

In some respects the results of the transition analyses are disappointing. The number of possible transitions was quite large. Thirty different movements were recorded in experiments 1-6, making 900 possible transitions in all. In experiments 7 and 8 there were thirty-two movements yielding 1,024 possible transitions. However, the proportion of transitions actually revealed by the screening procedure is not so unreasonably low as may appear at first sight. Firstly, the sign test criterion by which the screening procedure operated was quite severe with an n of 8 in each corpus of data. Secondly, only transitions noteworthy for their prominence featured in the results: for every entry in a transition matrix which contributed to the frequency in one cell exceeding its chance expectation, another cell must be one short of its expectation. Thirdly, in a $k \times k$ transition matrix, symmetry analyses can, at best, reveal as prominent only $(k^2 - k)/2$ out of k^2 possible transitions. Thus, a detection rate, based on the proportion of possible transitions revealed by the screening procedure, is a little misleading.

An additional consideration with the present set of data is that a few transitions, by definition, were impossible between adjacent movements. As, in the experimental pens, there was no shallow water in which the birds could stand, a standing movement could not be followed by a swimming movement (or vice versa) without an intervening "enter-water" (or "leave water"). A standing movement could not be followed by leave-water, nor a swimming movement by enter-water. And neither leave-water nor enter-water could occur in succession. This makes fourteen impossible transitions in all. Strictly speaking, the cells corresponding to these impossible transitions should have had their expected frequencies set to zero, with the expected frequencies in other

cells being adjusted accordingly, as explained in section 7.2.2 in relation to the cells on the diagonal of the transition matrix. In practice, neglect of this point will have made only a trivial difference to the results.

Despite the fact that a relatively small number of transitions was detected as noteworthy by the screening procedure, some of them are so prominent, turning up in many corpora of data, that they cannot be dismissed as chance findings. These transitions beg some kind of causal explanation. As has been emphasised, the transition analysis was descriptive rather than analytic. And although we now have available the results discussed in chapter 6 on external factors which facilitate the various movements, suggestions about the causal bases of sequential linkages are still necessarily speculative.

The transition swimming-flap to head-flick is as puzzling as it was when McKinney wrote his account of the comfort movements of the Anatidae. The results of chapter 6 showed minimal overlap in the effects of the experimental treatments on the two movements. It is easy to assert that the linkage must be endogenous in nature, but that is no more than a statement of ignorance about the mechanisms underlying the linkage.

The linkage bill-dip to head-shake could easily be interpreted as the result of a stimulus-response chain, with the bill-dip resulting in water on the bill which in turn elicited head-shake. No experiment has been carried out to test the effects of water on the bill. And the possibility that the whole sequence is compiled, so to speak, before the onset of the bill-dip, cannot be discounted lightly. Would anaesthesia of the bill disrupt the linkage?

The relations between different preening movements, especially

the dealing with one side of the body at a time, might be interpreted as the effects of "postural facilitation" (Tinbergen 1952). Expressed in terms of more modern ideas, the implication might be that some kind of optimisation rule is utilised which relates the urgency of preening a given area of the body surface to the "cost" of transferring from the target area presently being preened, to the new area. This would imply that a powerful enough stimulus from the body surface would outweigh the cost factor. Yet in the experiments, when rather powerful stimuli were applied, bilateral stimulation of certain areas (over wings, under wings, flanks) did not lead to a direct transfer from preening the relevant area on one side of the body, across to the relevant area on the other side of the body. The two "crossover" transitions which did feature in the results (7.3.3) were both between alternate movements. One was preen-flank-left to oil-right: here, oil-right is best interpreted as the start of a new preening sequence (McKinney). The other transition was preen-flank-right to preen-flank-left, but it was found not in the flanks experiment but when the chin area was subjected to detergent treatment: preening of the flank was not facilitated by treatment of the chin area. The results thus give no evidence that powerful bilateral stimulation can override the tendency to deal with several areas on one side of the body before transferring to the other side. It is difficult to envisage a much more powerful stimulus and so one is led to doubt the particular interpretation of the postural facilitation concept that is outlined above. On the other hand, it is quite clear that sequences of preening different areas of the body are not strictly fixed. It is thus particularly frustrating not to be able to look directly at the effects of the experimental treatments on the sequencing of comfort behaviour.

The linkages wherein head-shake was found to precede various

preening movements, more than it followed them, throws some doubt on the interpretation of head-shake as a response to soiling matter adhering to the bill as the result of preening. The three step sequence bill-dip to head-shake to preen (McKinney) does not account for the results as no evidence was found for bill-dip to precede preening in alternate movements. In fact, in transitions between adjacent movements, bill-dip showed a definite tendency to follow preening movements rather than vice versa. Thus bill-dip is more likely than head-shake to be a response to the soiling of the bill during preening. This belies a fairly strong impression from non-quantitative observations where it sometimes seems as though a bird bill-dipped in order to wet the bill for preening, as mentioned by McKinney.

The difference between head-flick, which is linked with scratching, and head-shake which is without such links, fits in with the pre-supposition that the two movements are radically different, and with the results reported in chapter 6 showing that they are facilitated by different types of peripheral stimulation. The linkages between head-flick and scratching are probably the most likely candidates, in the present data, for a symmetrical association between two movements on the basis of very little else other than their being elicited by similar factors. Interestingly, rub-over-wing, which has more in common with head-flick and scratching, seems to be linked asymmetrically with head-flick, in the order head-flick to rub-over-wing, and not at all with scratching.

The linkage head-dip to head-dip provided the only example in the data of a movement which was consistently found to follow itself in the majority of corpora of data. The time base used for data collection, based on time markers every ten seconds, precluded precise measurement of intervals between successive head-dips. Such an analysis might

throw some light on the control of series of head-dips, in terms of short-term increments and decrements consequent on performance (Hinde and Stevenson 1969).

The linkage head-dip to swimming-flap can be interpreted in terms of exogenous stimuli if it is assumed that head-dipping wets the wings and the back and that this, in turn, elicits the swimming-flap. However, this "explanation" leaves unanswered the question of whether the rising level of stimulation for head-flick resulted in the competitive suppression of head-dipping, or whether other factors leading to the cessation of head-dipping resulted in the disinhibition of swimming-flap (McFarland 1969). McFarland has argued that the two mechanisms of competition and disinhibition can be identified according to whether the time of occurrence of the second type of activity in a sequence can be manipulated by altering the level of its causal factors. If a temporal shift can be so achieved, the behavioural switch is thought to be based on behavioural competition between the two activities. It was not feasible to test directly for this kind of effect in the data generated by the experiments: too many factors varied over the duration of the observation session to make any findings interpretable one way or the other. A particular problem was that head-dips and swimming-flaps were found, in some experiments, to be facilitated by similar factors. This type of question needs to be answered in much simpler and constrained circumstances, such as were used in most of the experiments used by McFarland to illustrate his argument.

CHAPTER EIGHT

DISCUSSION

8.1 THE ROLE OF PERIPHERAL STIMULATION

The results of the experiments leave no doubt that peripheral stimulation can influence comfort behaviour in the mallard. This, in itself, is not surprising. More interesting is the information gained on the effects of localised peripheral stimulation on individual movements. It is not particularly surprising that treatment of a particular area of the body surface facilitated preening directed toward that area. From some points of view, however, more general effects would have been expected too, with preening of a number of areas being facilitated by treatment of a single area: such predictions were not upheld.

More interesting than preening, in the narrow sense of mandibulation or rubbing the feathers or bare parts, is the highly differentiated repertoire of shaking movements shown by mallard and other Anatidae. The data support some of the suggestions made by McKinney on the stimuli influencing particular movements, for example the elicitation of head-flick but not head-shake by treatment of the head plumage. On the other hand, the data do not support McKinney's notion that swimming-shakes are given (only) in response to wetting of the breast or his implication that standing-shakes ("body-shakes" in McKinney's terminology) are elicited by water on the plumage more generally. The experiments give a picture of swimming-shakes being influenced by treatment of a variety of areas of the body surface and standing-shakes by treatment of a more circumscribed region.

There are many sources of cutaneous stimulation other than that produced by wetting the plumage. Itching of the skin, of the kind caused by dirt and parasites, is one alternative source of stimulation. Another derives from the mechanical derangement of the feathers, presumably acting via receptors in the feather follicles. Such sources of

stimulation probably elicit different kinds of movement than wetting. Itching may elicit nibbling of the base of the feathers rather than long strokes whereby the bill is run along the length of the feather. And, as suggested by McKinney, mechanical derangement of the feathers may elicit body-shakes with much more wing vibration than is the case with wetting. Although alteration of the normal lie of the feathers probably contributes to the perception of wetting, the perception of wetting almost certainly requires more than just this: cooling of the skin, for instance, may be important. Thus the possibility must be borne in mind that conclusions drawn from wetting experiments might not apply to experiments which manipulated mechanical stimulation of the feathers or itching of the skin. If the effects of these various kinds of cutaneous stimulation did indeed differ from one another, then the notion that there was one primary causal factor underlying preening, or comfort behaviour in general, would be weakened even further.

8.2 THRESHOLD MODELS

Undoubtedly, the most influential suggestion that the causation of comfort behaviour could usefully be viewed in terms of a single causal factor comes from the work of ^{Van}/Iersel and Bol (1958) who, as described in section 3.6, postulated a preening drive which activated different movements at different thresholds.

It is quite clear from ^{Van}/Iersel and Bol's paper that they believed that, if their model had any explanatory power, a stimulus that augmented the level of the preening drive would facilitate not just one but several preening movements. Equally clearly, the results of the present series of experiments do not support this prediction. Different shaking and preening movements, both encompassed in ^{Van}/Iersel and Bol's usage of "preening", tended to be facilitated by specific changes in peripheral

stimulation of the kind obtained by wetting discrete areas of the body surface. The question remains: does this totally invalidate a multi-threshold single drive model of some kind?

The answer to this question is probably negative. There are so many alternative sets of assumptions that one could quite reasonably make about the operation of such a system that it is quite likely that a model could be constructed which could predict something like the obtained results.

To expand this point, any model system would need sets of assumptions to be made about a number of operating features. Among these are the following: the nature of the interaction between the level of the drive variable and the threshold of the various movements that it controls; the relationship between the level of the drive variable and the overall frequency of behavioural output; the way in which an external influence, e.g. an experimental treatment, affected the drive variable over time; and many more.

Consider, firstly, the nature of the interaction between the drive variable and the movement thresholds. Any movement with its threshold above the level of the drive variable would normally be considered wholly ineligible for activation, but what of "eligible" movements, that is, those with thresholds below the drive level? Four conceivable modes of operation will illustrate (but not exhaust) the possibilities.

1. All eligible movements are equally likely to be activated. This mode of operation is that used by Dawkins (1969) in his attention threshold model of choice behaviour.

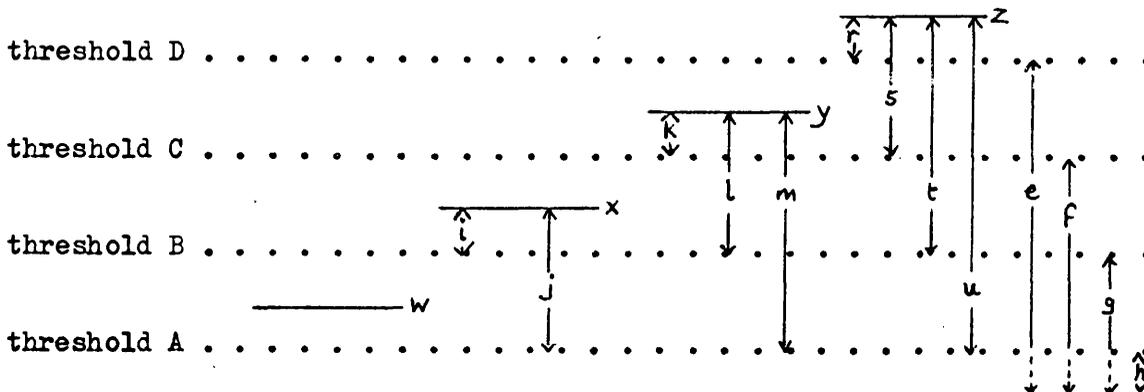
2. The probability that an eligible movement will be activated is directly related to the degree with which its threshold is exceeded by the drive variable. Thus, eligible movements with low thresholds

are preferred to eligible movements with high thresholds. This corresponds to the graded response principle used by Rowell (1960) in the model he proposed as an alternative to ^{v_{am}}Iersel and Bol's.

3. The probability that an eligible movement will be activated is directly related to the level of its threshold. Thus eligible movements with high thresholds are preferred to low threshold movements. This is roughly the opposite of model 2 and may be what ^{v_{am}}Iersel and Bol had in mind for their model.

4. The system is deterministic in that the only movement activated is the one with the highest threshold that is exceeded by the drive variable. The system could be made probabilistic by assuming that there were fast random fluctuations superimposed on slower changes in the level of the drive variable.

The following diagram illustrates the four models with reference to a system of four movements, A, B, C and D, where A has the lowest threshold and D the highest.



Let p_a , p_b , p_c and p_d stand for the proportionate rates of the four

movements so that $p_a + p_b + p_c + p_d = 1$ except when the drive variable is below the threshold for movement A in which case $p_a = p_b = p_c = p_d = 0$.

When the drive variable is at level w, $p_a = 1$ and $p_b = p_c = p_d = 0$ for all models.

When the drive variable is at level x, $p_a + p_b = 1$ and $p_c = p_d = 0$ for all models. The following relationships differentiate the models:

model 1: $p_a = p_b = 0.5$

model 2: $p_a : p_b = j : i$ i.e. $p_a > p_b > 0$

model 3: $p_a : p_b = h : g$ i.e. $0 < p_a < p_b$

Model 4: $p_b = 1$; $p_a = 0$.

When the drive level is at level y, $p_a + p_b + p_c = 1$ and $p_d = 0$ for all models. The following relationships differentiate the models:

model 1: $p_a = p_b = p_c = 0.33$

model 2: $p_a : p_b : p_c = m : l : k$ i.e. $p_a > p_b > p_c > 0$

model 3: $p_a : p_b : p_c = h : g : f$ i.e. $0 < p_a < p_b < p_c$

model 4: $p_c = 1$; $p_a = p_b = 0$

When the drive level is at level z, $p_a + p_b + p_c + p_d = 1$ for all models. The following relationships differentiate the models:

model 1: $p_a = p_b = p_c = p_d = 0.25$

model 2: $p_a : p_b : p_c : p_d = u : t : s : r$ i.e. $p_a > p_b > p_c > p_d > 0$

model 3: $p_a : p_b : p_c : p_d = h : g : f : e$ i.e. $0 < p_a < p_b < p_c < p_d$

model 4: $p_d = 1$; $p_a = p_b = p_c = 0$.

The predictions from the models, based on proportionate rates of different activities, are quite straightforward. However, to acquire data in terms of proportionate rates it would be necessary to know the identity and number of all the different activities controlled by the system. But this is very often the subject of enquiry. Thus, for the

models to be of much use, predictions should be stated in terms of crude frequencies of the different movements.

To derive from the models predictions concerning the frequency of occurrence of various movements, rather than proportionate rates, it is necessary to consider how the overall rate of responding is related to the level of the drive variable. In his attention threshold model, Dawkins (1969) assumed overall response rate to be independent of the level of the drive variable. More usually, however, drive intensity is thought to affect overall response rate in a direct manner. A linear relationship between drive level and overall response rate implies non-monotonic relationships between drive level and the frequency of individual movements in all but the second of the four models discussed. In other words, augmenting the drive variable would be expected to affect the frequency of individual movements in complex ways.

Iersel and Bol used overall response rate as an independent measure of drive level and deduced that drive fluctuated over time in a fairly complex way. Presumably, therefore, an experimental treatment would be thought to change drive not merely by raising its level to a new steady state, but also in a dynamic manner, by altering its rate of change. The nature of this alteration is yet another feature of a model that would have to be specified or deduced in order to predict, from a model, the expected effects of experimental treatments.

At this stage it is apparent that there is little to be gained by trying to fit some kind of threshold model, for which there are so many unknowns, to the data generated by the experiments. Even without adding further complications, such as moveable thresholds (c.f. Andrew 1961), it is likely that some kind of model could be generated to fit almost any sort of effects the experimental treatments might have had on the

frequency of different movements.

This conclusion has implications for the thorny problem of deciding which movements are supposed to be included in a system to be modelled. How could one decide whether shaking, preening and bathing movements are all controlled by a single system of this kind, by two, by three or by more distinct systems? The possible criterion of whether or not the various movements are similarly influenced by an experimentally manipulated factor seems to be unusable. One might expect the individual movements controlled by a single multiple-threshold system to form a so-called Guttman scale whereby the occurrence of a movement should be associated with the occurrence of all movements with lower thresholds. Model 4, however, certainly does not have this property, even the probabilistic version.

It should not be inferred that threshold models, or models of other kinds, are of course whatsoever. The work of Dawkins and of McFarlane (1971) shows that this is not the case. However, successful models are generally simple, precisely specified, and include relatively few alternative movements. In the case of comfort behaviour, or even a restricted subset such as that described by ^{van}Iersel and Bol, there is a relatively large repertoire of movements. Moreover, ^{van}Iersel and Bol's model was not clearly specified.

As far as the experiments go, it must be concluded that a prediction made by Iersel and Bol is not upheld, but the operation of a multi-threshold single drive system is not tested by the data. Indeed, the heuristic potential of such a model, applied to comfort behaviour, is limited.

One final point is also relevant. Fentress (1972, 1976) has argued forcefully that boundaries between behavioural systems are, in all

likelihood, dynamic. More specifically, Fentress presents evidence that as the level of activation of a control system increases, the variety of activities under the influence of that system decreases. Although such an effect could be described in terms of a threshold model with rather peculiar operating characteristics, it is clearly contradictory to the predictions of the four models described above. If an experimental treatment was fairly strong, specific rather than general effects would be expected under Fentress' scheme.

8.3 TEMPORAL AND SEQUENTIAL ORGANISATION

The experimental technique of wetting the feathers with a detergent solution was extremely successful in producing a spatially localised effect which had no observable lasting effect on a time scale of the order of hours. Nonetheless, a technique with more potential for experimental control over the temporal aspects of stimulation will be required in order to solve many of the more interesting problems in the causation of comfort behaviour, especially problems concerning its sequential organisation.

There can be little doubt that, in general, the performance of a comfort movement reduces peripheral stimulation of the kind most likely to be involved in the elicitation of that movement. Therefore, the stimulus situation of an animal engaged in comfort behaviour will change from moment to moment. In view of this, it is not surprising that, as shown by the sequential analysis, runs of the same kind of movement tend not to occur, the exception being head-dip. Changes in behavioural output from moment to moment may not be due solely to changes in the balance of peripheral stimulation: short-term endogenous changes consequent on the performance of a given movement (Hinde and Stevenson 1969) doubtless play a role too. Nonetheless, the likelihood of short-

term changes in peripheral stimulation means that, for experimental analysis to progress, techniques must be found for the experimental control of short-term phasic influences.

Peripheral stimulation could influence the output of comfort behaviour at a number of causal levels. It is worth considering, in particular, the possible roles of exogenous factors in the more fine grained motor control of preening and other movements. Consider, for instance, the type of preening where a long feather is drawn through the bill from base to tip. Once started, does such a stroke "run off" as if under ballistic control, or can it be modified by, say, tactile stimuli received from the feather as it is run through the bill? And would tactile stimulation received on one stroke affect the next?

In a similar vein, consider the various components of the body-shake, namely movements of the tail, wings and head as described in chapter 4. One or more of these components may be missing from a body-shake. Can exogenous factors be found to account for this variability? Questions such as these provide fertile ground for future investigation.

Finally, it should not be inferred that the emphasis on peripheral factors means that endogenous causal factors are considered unimportant. This is clearly not the case in view of the ease with which comfort behaviour seems to be inhibited by other tendencies. The precise nature of the interactions with other tendencies remains poorly understood but a better understanding of exogenous factors may well provide means of analysis with which to attack the problem. This point is underscored by the studies discussed in chapter 3 where the manipulation of peripheral input has been employed to analyse interaction of irrelevant comfort behaviour with other tendencies.

8.4 SOME COMMENTS ON THE RITUALISATION OF COMFORT MOVEMENTS

When, in the course of evolution, comfort movements differentiate so that a version of the movement becomes specialised to serve as a signal, it is axiomatic that there must be differentiation of the causal factors producing the primary form of the movement and its derivative display form. The display is said to have become fully or partially "emancipated" from the factors controlling the production of the movement in its primary form. Blest's (1961) discussion of emancipation shows how tricky this concept has been to work with beyond the axiomatic and descriptive levels; nonetheless, it has an essential role in any theoretical approach to the evolution of displays from pre-existing movements. One reason for the lack of progress is the slow accumulation of detailed knowledge of the causation of displays and their non-display precursors.

As with their precursors, the causal factors for displays act at a number of different levels. On a time scale of seasonal reproductive cycles, many displays, not just those that are clearly epigamic in function, are known to be under hormonal control. One aspect of the process of emancipation that is rather difficult to imagine is a stepwise emergence of endocrine influence on a comfort movement as it evolves into a display. It is tempting to look for factors in the causation of the primary form of the movement that could be pre-adaptive in this respect. Endocrine factors control moult, and the secretion of preen-oil from the uropygial gland is known to be under hormonal influence (Kar 1948). Moult and preen-oil production probably affect comfort behaviour in various ways, including via cutaneous sensory input (McKinney). Such effects could conceivably have provided the initial "evolutionary toehold" on the basis of which hormonal influences have assumed a more important role in the causation of ritualised comfort

movements.

Toward the other end of the spectrum of levels of causation there is the control of motor co-ordination. Changes in co-ordination accompanying the emergence of a display are among the most thoroughly discussed aspects of ritualisation. Morris (1957) lists a number of types of difference in co-ordination between displays and their precursors, including changes in the orientation of the movement, changes in speed of performance, the development of rhythmic repetition, differential exaggeration of components, omission of components, and changes in their co-ordination and sequencing. A detailed comparative analysis of the mechanisms of motor control of a display and its precursor would probably be very illuminating. As Blest (1961) suggests, the outcome might not be very different from conclusions regarding evolutionary changes in locomotory mechanisms. Preen-behind-wing displays of the Anatidae would probably prove particularly suitable material for such an analysis, starting with the effects of cutaneous input on the co-ordination of functional preening, as suggested in the previous section.

With regard to changes in orientation, a lead suggested by Simmons and Weidmann (1973) should certainly be followed up. The orientation of shaking movements seems to be affected by visual cues, especially those from conspecifics. Here there is continuity between comfort movements and highly ritualised displays such as the grunt-whistle.

The other major point of focus on the relationship between ritualisation and the causation of behaviour concerns the role of motivational conflict (Baerends, 1975). This is particularly important in cases where displays are thought to have evolved from displacement activities. Both the original hypothesis of a "sparking-over of motivational energy" and the more recent disinhibition hypothesis stress

the importance of motivational conflict, although there is some dispute as to whether this is best understood in terms of major tendencies like attack, flight and mating (Morris 1956) or particular responses subsumed under these global tendencies (Andrew 1972) - each view seems to have strengths and weaknesses (Hinde 1974). Motivational conflict of one sort or another features prominently in most causal accounts of display, a clear continuity with displacement precursors.

Now according to the disinhibition hypothesis, apart from the origin of the disinhibitory process, a displacement activity is subject to the same causal influences as the same activity in non-displacement contexts. The nature of the relevant external stimuli may explain the prominence of comfort movements as displacement activities, particularly among water birds. Situations in which displacement activities are recognised arise during periods of fairly vigorous activity when the plumage is likely to be disturbed and subjected to wetting. Such peripheral influences probably tip the balance and ensure that comfort movements rather than, say, feeding actions, are disinhibited by motivational conflict. Indeed, external stimulation may sometimes be strong enough for comfort movements to appear through competitive interaction with other tendencies or responses (McFarland 1968) rather than by disinhibition.

It would seem that, in the course of evolution, displays have become less dependent on external stimulation. Or at least, cutaneous input is replaced by external stimulation of a different kind, emanating from companions in a social context. Some displays which are minimally ritualised in terms of changes in their form, may well be open to both kinds of influence. Or at least, a movement produced by cutaneous stimulation may be minimally different perceptually from a movement

elicited by social influences. This raises what is perhaps the most intriguing possibility to come out of the present study. The swimming-shake, which is very similar indeed to the "introductory-shake" display can be brought under experimental control. Can experimentally induced swimming-shakes have the same social effects, in a party of courting males, as the introductory shake? If so, we would have an extremely useful tool for analysing the social effects of this display, and a methodology that might be extended to other displays too.

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