

**Polygyny, parentage and parental
investment in the
corn bunting, *Miliaria calandra***

Thesis submitted for the degree of
Doctor of Philosophy
at the University of Leicester

by

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For Mum and Dad

Tresspass, let it be repeated, is not a crime prevalent among males. Each bird is too much concerned with the possession of his own perch and with the doings of his own hens to bother himself much over neighbouring males or their mates.

We have no record of a male molesting, amorously, another's hen.

Ryves and Ryves (1934)

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Abstract

Polygyny, parentage and parental investment in the corn bunting, *Miliaria calandra*.

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1) This study investigated the costs and benefits of a polygynous mating system, and its effects on reproductive success and parental care in male and female corn buntings (*Miliaria calandra*), on North Uist, Outer Hebrides. In 1989 and 1990, 41.2% of males were monogamously paired, 33.3% polygynous and 23.5% unpaired; the sex ratio was 1:1. Polygynous males usually paired with two females; occasionally three. The distribution of females among males was not significantly different from a binomial distribution.

2) DNA fingerprinting showed that there were only two possible cases of extra-pair paternity (EPP) due to extra-pair copulation (EPC) (4.5% of 44 offspring; 6.7% of broods), both from the same brood. There were no cases of intra-specific brood parasitism (IBP) (0% of 50 offspring; 0% of 16 broods). EPP was probably rare because of mate guarding by the male, asynchrony between broods for polygynous males and limited opportunities for EPC. Polygynous males fledged more offspring from their territories than did monogamous males because they paired with more females; unpaired males fledged no offspring.

3) Unlike most other polygynous birds, primary and secondary females of polygynous male corn buntings had similar reproductive success and both had greater reproductive success than monogamous females. Monogamous females had lower reproductive success because their chicks starved more often. Although monogamous females provisioned nestlings at a similar rate to females of polygynous males, monogamous females delivered smaller food loads, which may have led to the reduced success of those nests.

4) Males rarely fed nestlings before they were four days old. Males provided less food for nestlings than did females at all chick ages and, on average, provided a maximum of only 22.0% of all feeds. Unusually for a polygynous species, males provisioned nestlings of monogamous, primary and secondary females with similar sized food loads and at similar rates.

5) Broods belonging to primary and secondary females were apparently equally valuable to their males because EPP was low in this population and brood sizes were similar between nest classes. Males may have been able to feed both nests because they were temporally separate, although at least one male was able to feed overlapping nests simultaneously. Males provisioned proportionately less than females at early stages of the nestling period, possibly because of sex differences in other available reproductive opportunities. Females had no better available option than to provide parental care to the current brood, whereas males could potentially increase their fitness better by defending a territory in which females could breed.

6) Males appeared to defend areas in which females chose to nest rather than to forage. Females often foraged outside male territories. The territories of unpaired, monogamous and polygynous males did not differ significantly in habitat composition.

7) Female corn buntings neither suffered costs to polygyny, nor did they compete for resources, such as male parental care, nest sites or food. Nests were under-dispersed in space, because of habitat aggregation, and were randomly dispersed in time within territories. Primary and secondary females of polygynous males did not choose territories in the same order, and the first settling females of polygynous males did not settle significantly earlier than monogamous females; this suggests that males were chosen randomly, rather than by the quality of their resources. I suggest that low variance of male territory quality facilitated random female choice of males. A no-cost, no-benefit model, with females choosing males randomly is suggested as the best explanation for the maintenance of polygyny in the corn bunting.

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Chapter 1. General introduction

1.1. Introduction

1.2. The corn bunting

1.3. Duration of study and study site

1.4. General methods

1.4.1. Assigning mating status and nest status

1.4.2. Catching adults

1.4.3. Processing trapped birds

1.4.4. Statistical tests

1.5. Outline of chapters

1.1. Introduction

Animals are expected to maximize their reproductive success under the current or past influence of natural or sexual selection (*sensu* Darwin 1859, 1871; Dawkins 1982). Individuals are also expected to behave selfishly to achieve this end (Dawkins 1976), which includes taking advantage of other individuals, where possible, to increase reproductive success. The measurement of reproductive success has been the cause of much interest recently, especially with the advent of molecular techniques to identify true, genetic parentage of individuals, and the conflict of interests between the sexes is a major factor which needs to be included in its consideration (Trivers 1972; Davies 1991). Males, for example, could potentially gain most from maximizing the number of matings with females, whereas females should seek the fullest involvement of males in parental care.

In his classic review of mating systems in birds, Lack (1968) found that 90% of bird species were monogamous in that one male paired with one female to rear offspring. He suggested that monogamy was so predominant because both males and females of most species achieved the highest reproductive success when they paired monogamously. Since Lack's original hypothesis, male removal experiments have shown that, in many monogamous species, females do not increase their parental care (e.g., feeding rates) to compensate totally for the loss of male parental care, and so a decrease in reproductive success is observed (e.g., Oring 1982; Smith *et al.* 1982; Greenlaw and Post 1985; Houston and Davies 1985; Lyon *et al.* 1987; Wolf *et al.* 1988; Wright and Cuthill 1989; Bart and Tornes 1989; Hatchwell and Davies 1990). Lack's prediction was that each sex should achieve greatest fitness through monogamy, however, if females only suffered a partial reduction in breeding success due to the removal of the male, a better option for a male should be to abandon his first female, leaving her to rear the young alone, and then pair with a second female and help her to raise their young. The male would, therefore, gain from one full brood plus a partial brood reared by the deserted female, and if he could

continue to obtain further females he would increase his success further, by a partial brood for every female he paired with. Lack was clearly not correct in suggesting that each sex would maximize its reproductive success by being monogamous, and his observation that 90% of bird species are monogamous requires explanation.

In the situation described above, females suffer from reduced reproductive success when paired to a polygynous male, and so should choose to pair monogamously. Female-female aggression could prevent other females from settling with already paired males and male-male competition could make it impossible for males to acquire more than one female (e.g., one male may not be able to successfully defend sufficient resources for more than one female). In a review of mating systems in passerine birds, Møller (1986) showed that 39% of 122 well studied species were occasionally polygynous. This reflects the fact that, under certain circumstances, males can potentially become polygynous, but why are some species regularly polygynous?

Polygyny can occur as a regular aspect of a species' mating system for several reasons:

1) If resources such as food or nest sites are aggregated, it may be possible for some males to defend disproportionate amounts of resources needed by breeding females. If females settle according to available resources some males may become polygynous.

2) A female may be able to provide all the necessary parental care to succeed in rearing her offspring alone, probably because of the availability of good quality foraging sites, and so males may be emancipated from parental care. This can lead to polygyny by two routes: either males have more time to attract more females or females no longer need to take male parental care into account when settling to nest and may do so randomly with respect to males, so that some males become polygynous by chance or by defending high quality breeding areas.

3) Females may accept polygyny, despite it being less productive for them than monogamy, because either no unmated males are available, or they cannot tell whether a male is paired or not within a suitable period of time, or they are unable to monopolize a male against other females through female-female aggression.

In birds, polyandry is much rarer than polygyny (Oring 1982), possibly because birds have internal fertilization and males can fertilize eggs faster than the females can produce them. Males are, therefore, likely to be less certain of their paternity than females are of their maternity and so females are more likely to be left 'holding the baby' because males always have the option of deserting first (Clutton-Brock 1991). Opportunities for further matings are also likely to be greater for males for similar reasons (Davies 1991).

Trivers (1972) suggested that males and females which are unable to gain extra mates by pair-bonding should seek extra reproductive opportunities by other methods, such as males obtaining sneaky copulations with other males' females (extra-pair copulation, EPC) or females dumping eggs in the nests of conspecific females (intra-specific brood

parasitism, IBP). Such 'mixed reproductive strategies' have been shown to occur in several apparently monogamous species (reviews in Yom-Tov 1980; Birkhead *et al.* 1987; Westneat *et al.* 1990; Petrie and Møller 1991). These alternative reproductive strategies can be successful in adding to an individual's fitness, as has been shown using techniques such as vasectomized territorial males (Bray *et al.* 1975), genetic plumage markers (Cooke and Mirksy 1972; Burns *et al.* 1980; Birkhead *et al.* 1989; Lank *et al.* 1989), sexual differences, between the parents, for heritabilities of morphological traits in the offspring (Alatalo *et al.* 1984b; Møller 1987a; Norris and Blakey 1989; Payne and Payne 1989; but for serious criticisms of this approach see Dhondt 1991; Henrich and Nager 1991), allozyme analysis (e.g., Gavin and Bollinger 1985; Mumme *et al.* 1985; Evarts and Williams 1987; Wrege and Emlen 1987; Bollinger and Gavin 1991) and DNA fingerprinting (Jeffreys *et al.* 1985a, b; Burke and Bruford 1987; Wetton *et al.* 1987; Birkhead *et al.* 1990; Gibbs *et al.* 1990; Morton *et al.* 1990; Westneat 1990; Wetton and Parkin 1991; but see Gyllenstein 1990 and Hunter *et al.* in press). The recent use of DNA fingerprinting (Jeffreys *et al.* 1985a, b) has revolutionized this work, because it is now possible to identify parents and non-parents of offspring more accurately than ever before (Burke 1989).

Being cuckolded by EPC or IBP is potentially very expensive for a breeding bird. The costs of reproduction are high (Clutton-Brock 1991), especially in species with altricial young which require feeding and brooding by one or more adults, so parents should ensure that all their parental care is directed towards their own offspring rather than those of other individuals. To reduce the chances of cuckoldry, males could mate guard their females during the fertile period to ensure that other males cannot copulate with her, or if guarding is not economically viable, males may use frequent copulation as a method of ensuring paternity of their brood (review in Birkhead *et al.* 1987).

In polygynous species, males may have to divide mate guarding effort between two or more females and so certainty of paternity may be variable between nests of the same male (Arak 1984; Davies 1991). Møller (1988, 1991a, b) has shown that males of the monogamous barn swallow reduce paternal care when they are less sure of their paternity, and alpha and beta males within polyandrous trios of dunnocks balance their paternal nest provisioning effort against their certainty of paternity of the brood (Burke *et al.* 1989). No previous studies have investigated the effects of uncertainty of paternity on male parental care in a polygynous species.

This study uses the polygynous corn bunting and DNA fingerprinting to investigate several aspects of polygyny:-

- 1) Is polygyny really the most successful pairing state for a male or do mixed reproductive strategies of other males reduce the reproductive success of polygynous males so that they are similar to monogamous or unpaired males?

2) How do females suffer from polygyny, if at all, in terms of reduced reproductive success?

3) How is parental care affected by certainty of paternity of the male?

4) How does availability of resources affect where, and with which males, females should nest?

5) How is polygyny maintained in corn buntings in comparison with other territorial bird species?

1.2. The corn bunting

The corn bunting is the largest member of the *Emberizidae*. Males are larger than females by approximately 20% (Female : male weight = 1 : 1.22, Møller 1983; Svensson 1984) but otherwise sexes appear similar, unlike in other *Emberizidae* species (Catchpole and McGregor 1985). It has been suggested that the size dimorphism, and lack of plumage dimorphism, is a result of intra-sexual selection benefitting larger males in the corn bunting (Catchpole and McGregor 1985). This idea would fit in with the highly territorial nature of the corn bunting's breeding system, where males would benefit from being larger if size conferred an advantage to territory holders.

Despite being relatively common and widespread (Sharrock 1976; Lack 1986; Marchant *et al.* 1990), there are few published studies on the corn bunting's reproductive behaviour and polygynous mating system. Breeding studies have been carried out, to varying degrees, in Sussex, England (Walpole-Bond 1931, 1938), Cornwall, England (Ryves and Ryves 1934a, b), Dorset, England (Gyllin 1965, 1967), Sutherland, Scotland (MacDonald 1965), Germany (Gliemann 1972) and Switzerland (Hegelbach and Ziswiler 1979; Hegelbach 1984), although none of these studies has closely examined reproductive success in relation to the mating system. Ryves and Ryve's (1934a, b) study was a classic for its time because it was the first to quantify the extent of polygyny in a passerine. Lack (1968) was, however, sceptical that corn buntings were actually polygynous because their study was not based on colour-ringed birds. Only Hegelbach's (Hegelbach and Ziswiler 1979; Hegelbach 1984) and Gliemann's (Gliemann 1972) studies have used individually ringed birds but these were mainly concerned with the population dynamics, singing behaviour and territorial behaviour of the species. Most studies have concentrated on corn bunting song dialects and male singing behaviour (Gyllin 1967; Czikeli 1980, 1982; McGregor 1980, 1983, 1986; Pellerin 1981, 1982, 1983; Møller 1983; Catchpole and McGregor 1985; McGregor and Thompson 1988; McGregor *et al.* 1988; P.K. McGregor and M. Shepherd pers. comm.). Other studies have been mainly based on the results of population size and distribution surveys (Goodbody 1955; Williamson 1968; Terry 1986; Williams *et al.* 1986) but did not examine behavioural ecology or breeding behaviour.

In recent years, the corn bunting population in Britain has undergone a national decline

(Sharrock 1976; O'Connor and Shrubbs 1986; Marchant *et al.* 1990), following a general trend for seed-eating passerines inhabiting agricultural habitats (Marchant *et al.* 1990). The decline has closely followed the reduction in national acreage of barley grown on farms (Harrison *et al.* 1982), but whether this link is causal or correlational is far from clear (Thompson and Gribbin 1986; O'Connor and Shrubbs 1986). O'Connor and Shrubbs (1986) suggested that the decline may be caused by a general increase in intensification of farming practice and the consequent increase in the use of herbicides, and decrease in autumn stubble and spilled grain, although Thompson and Gribbin (1986) suggested that barley is important as a nesting and foraging habitat for breeding corn buntings.

Typically, for a bird which occupies an agricultural habitat yet is not a pest, there have been few studies on the habitat use and requirements of corn buntings and, despite its interesting polygynous mating system, first referred to by Walpole-Bond (1931) and Ryves and Ryves (1934a, b), the breeding behaviour and mating system of the corn bunting have not previously been studied in detail.

1.3. Duration of study and study site

The field study was carried out during the periods early May to the end of August, in 1989 and 1990, at Balranald (57° 37'N, 7° 30'W), on the west coast of North Uist, Outer Hebrides, Scotland (Fig. 1.1). The study area (Fig. 1.1) consisted of a 7 km² coastal strip of shell-sand soil, farmed on a three or four year rotation basis. This sandy, cultivated land, unique to the Outer Hebrides and known locally as 'machair' (Fuller 1982), was mainly used to grow cereal crops (barley and rye) for cattle feed. Fallow areas, which were not currently under cultivation, were usually grazed by cattle. Vegetation on the coastal edge ridge was dominated by marram (*Ammophila arenaria*) on the seaward side and a hogweed (*Heracleum sphondylium*) dominated, hogweed/marram mixture on the land side. The study site was chosen because, unlike in other areas of Britain (P.K. McGregor pers. comm.), all nests were accessible without having to enter cultivated crops and it was one of the few areas in Britain where corn buntings were not apparently declining in numbers (Sharrock 1976; O'Connor and Shrubbs 1986).

1.4. General methods

1.4.1. Assigning mating status and nest status

Males were assigned to one of the categories unmated, monogamous, bigamous or trigamous in any one year. These categories referred to the number of females, per breeding season, that settled on the males' territories and stayed to build a nest and lay eggs. Females were sometimes seen on several territories but were not considered to be mated to a male if they did not stay to lay at least one egg on his territory.

Female status was assigned according to her nest status in relation to other females on

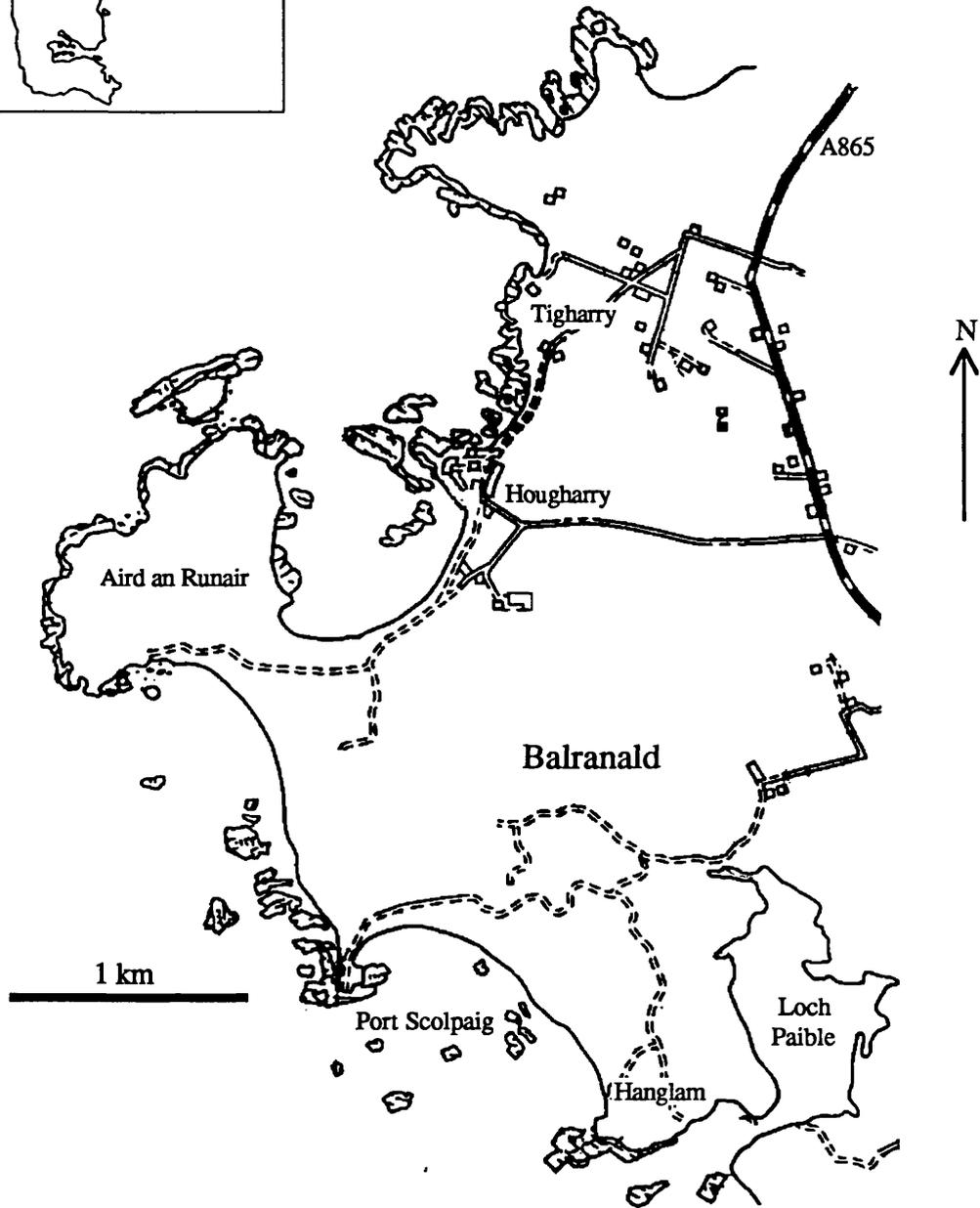
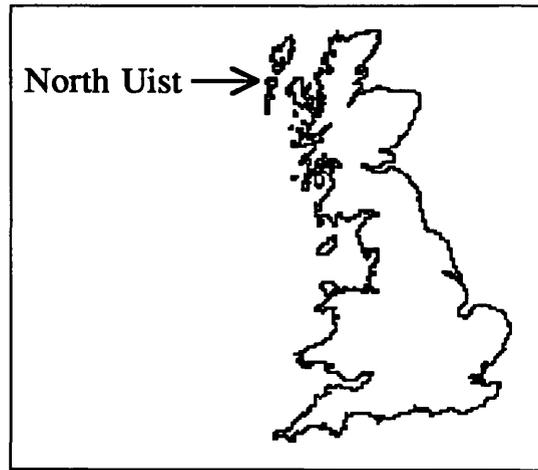
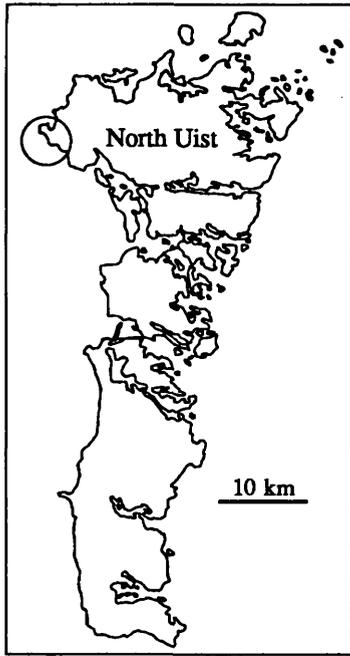


Fig. 1.1. Location of North Uist and Balranald. The study site was approximately all land which was west of a line between the north end of Loch Paible and Hougharry.

the territory. Monogamous refers to a female which was the only female paired with a male, primary refers to the first female of a polygynous male, secondary the second and tertiary the third. No males had more than three females in any one year of the study.

The nest categories monogamous, primary and secondary were assigned independently of the male's status and two methods were used. For examination of overall nesting success, including nests which failed prior to hatching, I used any overlap of the whole nesting cycle for nests on the same territory. This included from six days before first egg date to 20 days after fledging as the nesting cycle because the females were effectively breeding during this period. Monogamous nests had no overlap over the breeding period of approximately 52 days. Primary, secondary and tertiary nests were temporally overlapping nests, where the primary was the first with eggs, the secondary the second and so on.

The second definition of nest status was derived from reference to the overlap of the period that chicks were in the nest plus a 20-day fledgling period. A nest which was secondary at first egg date could become monogamous, or even primary, if the other female on the territory fledged her chicks or failed and had to relay. The second definition was more exact in terms of comparisons of nest provisioning behaviour (chapter 4), but nests failing before hatching could not be assigned by this method, so the first definition was used for all nests when comparing breeding success parameters (chapter 3).

A first clutch was defined as a female's first nest, with eggs, in one breeding season, a relay was a replacement nest, with eggs, of a female whose previous attempt was known to have failed and a second brood was a subsequent nest, with eggs, of a female known to have fledged young from a previous nest in the same breeding season. Only three out of 83 nests could not be assigned to one of these three categories and, of those three, one was definitely not a first clutch and one was not a relay. All male territories and all female nesting attempts (apart from one, in 1990) were monitored throughout the season.

1.4.2. Catching adults

All birds were trapped under licence from the Nature Conservancy Council and British Trust for Ornithology (BTO). Breeding females were trapped by two people carrying a mist net over the nest and dropping it onto a female while she brooded chicks. This was done at dawn, when the female was still brooding the young from the previous night, but not before the chicks were four days old, as before that age there was a risk of desertion.

Males proved extremely difficult to trap, especially as simultaneous work on reactions to song playbacks meant that tape lures could not be used early in the season, despite a generally good response (M. Shepherd pers. comm.). Most males were either ringed as chicks in the nest or were trapped in the winter at roosting sites, either by dazzling, drag-netting (Davis 1981) or occasionally mist-netting.

1.4.3. Processing trapped birds

Birds were ringed with a BTO, numbered metal ring and three colour rings in combination (two rings per leg). They were measured, according to Svensson (1984) and Spencer (1984), for wing length to the nearest mm (maximum chord, flattened) and weighed to the nearest 0.1 g. Tarsus was measured, to the nearest 0.1 mm using vernier calipers, from the posterior notch at the intertarsal joint to the front of the tarsal bone with the toes bent down (Henderson 1991). All birds were blood-sampled from the brachial vein under Nature Conservancy Council and Home Office licence. Corn buntings undergo a complete post-juvenile moult in the autumn, at the same time as the adults undergo a complete post-nuptial moult, so adults are impossible to separate from first year birds after about September (Ginn and Melville 1983).

Breeding females were marked for sex determination during the nest watches (chapter 4) using white typists' correction fluid (Tippex) on several secondary wing coverts. This enabled birds to be sexed in flight, as well as when perched, without having to read the colour ring combination. This type of mark was not permanent but lasted longer than the nestling period.

1.4.4. Statistical tests

Unless otherwise stated statistical tests follow Rohlf and Sokal (1981), Sokal and Rohlf (1981), Siegel and Castellan (1988) and the Statview 512+™ package produced by Abacus Concepts, Inc.. All tests are two-tailed and are corrected for continuity, or tied ranks, as appropriate.

1.5. Outline of chapters

This study investigates the effects of a polygynous mating system on the actual reproductive success of males (chapter 2) and females (chapter 3) in the corn bunting. DNA fingerprinting is used to determine the extent of the use of mixed reproductive strategies in both males and females. Parental care and the relative contributions of each sex are described in relation to polygyny and parentage (chapter 4). Habitat structure of male territories is analysed with respect to the nesting and foraging needs of females and its role in the maintenance of polygyny and populations in the corn bunting (chapter 5). Current polygyny models are reviewed and discussed in relation to corn bunting polygyny in order to understand how polygyny occurs in this, and other, species (chapter 6).

Chapter 2. Male reproductive success and extra-pair parentage in males and females

2.1 Introduction

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2.5. Summary

2.1. Introduction

In recent years there has been an expanding body of published literature concerning the occurrence of mixed reproductive strategies (Trivers 1972) in birds (reviews in Birkhead 1987; Birkhead *et al.* 1987; Westneat *et al.* 1990). A mixed reproductive strategy is one in which an individual maximizes its reproductive success by seeking alternative reproductive opportunities in addition to raising some offspring itself (Trivers 1972). In birds, these alternative strategies are extra-pair copulation (EPC) by males attempting to father offspring which will be reared by other pairs (Birkhead *et al.* 1987), and intra-specific brood parasitism (IBP), or egg dumping, by females which lay eggs in nests other than their own, for the young to be raised by other females or pairs (reviewed by Yom-Tov 1980, updated by MacWhirter 1989). There should be opposing selection pressures on the evolution of such mixed reproductive strategies, because even though males should increase their fitness by obtaining many EPCs, and females should increase theirs by dumping many eggs, there will be an evolutionary counterbalance which should increase the hosts' abilities to assure the paternity and maternity of the offspring in which they invest parental care (Trivers 1972). The chances of assuring paternity could be increased by mate guarding during the fertile period (e.g., Birkhead 1982; Birkhead *et al.* 1985,

1990; Björkland and Westman 1986; Alatalo *et al.* 1987; Møller 1987b, c), frequent copulation (Møller 1987d; Birkhead and Lessells 1988) or, in species where last sperm precedence may be important (e.g., Birkhead *et al.* 1988, 1989; Hunter *et al.* in press), obtaining the last copulation prior to fertilization. Females could increase their chances of assuring maternity by own-egg recognition and discrimination against 'foreign' eggs (Petrie and Møller 1991).

Until recently, the relative importance of mixed reproductive strategies was not measurable in wild bird populations in the field because true, genetic parentage could not be assigned to offspring. Recent advances in genetics have provided DNA fingerprinting (Jeffreys *et al.* 1985a, b) as a tool to determine actual paternity and maternity for individual offspring, and the technique has already been applied in several studies of birds (e.g., Burke and Bruford 1987; Wetton *et al.* 1987; Burke *et al.* 1989; Westneat 1990; Gyllensten *et al.* 1990; Birkhead *et al.* 1990; Morton *et al.* 1990; Gibbs *et al.* 1990; Jones *et al.* 1991; Lifjeld *et al.* 1991; Smith *et al.* 1991; Wetton and Parkin 1991; Hunter *et al.* in press). Reported extra-pair paternity (EPP) rates vary widely between species, from 55% of offspring in reed buntings (A. Dixon pers. comm.) to 0% for wood warblers and willow warblers (Gyllensten *et al.* 1990) and fulmars (Hunter *et al.* in press) (Table 2.1).

There has been a noticeable lack of studies of parentage in polygynous species (Table 2.1), and two of those studied so far - pied flycatchers (Lifjeld *et al.* 1991) and wood warblers (Gyllensten *et al.* 1990) - are polyterritorial polygynists, which is a relatively rare form of polygyny. Red-winged blackbirds are highly polygynous, with males pairing with up to 10 females (Lenington 1980), but the high rate of EPP means that the observed reproductive success of males is incorrect (Gibbs *et al.* 1990). More studies of true parentage for polygynous species would be useful when trying to draw general conclusions about the relative fitness gains of individuals in different pairing situations.

This chapter describes genetic parentage for the corn bunting study population, using DNA fingerprinting, and in particular asks whether polygynous males suffer a higher rate of EPP in broods belonging to secondary females. This could arise if males reduced attendance to their secondary females, when they might be fertile, in favour of attending to the nest of the primary female or the primary female herself (Arak 1984). Do males pairing with more than one female really have a higher reproductive success than males which remain monogamous or unpaired, or are corn buntings genuinely promiscuous - such that females copulate with several males prior to laying - as has been suggested elsewhere (Hegelbach and Ziswiler 1979; Møller 1983; Hegelbach 1984)?

	n offspring tested	% EPP	% IBP	Mating system#	reference
Fulmar	91	0	0	m,c	Hunter <i>et al.</i> in press
Oystercatcher	23	5	0	m	Ens <i>et al.</i> unpublished
European bee-eater	100	1	0	m,c	Jones <i>et al.</i> 1991
Barn swallow *	45	22.2	0	m,c	Smith <i>et al.</i> 1991
Purple martin	52	18	17	m,c	Morton <i>et al.</i> 1990
Pied flycatcher	135	4	0	pt	Lifjeld <i>et al.</i> 1991
Dunnoek	133	<1	0	pa	Burke <i>et al.</i> 1989
Willow warbler	120	0	0	m	Gyllensten <i>et al.</i> 1990
Wood warbler	56	0	0	pt	Gyllensten <i>et al.</i> 1990
Red-winged blackbird	111	28	0	pm	Gibbs <i>et al.</i> 1990
Zebra finch	92	2.4	11	m,c	Birkhead <i>et al.</i> 1990
Starling	58	10.3	0	pm,c	Hanotte 1991
House sparrow	536	13.6	0	m,c	Wetton and Parkin 1991
Indigo bunting	63	35	0	m	Westneat 1990
Reed bunting	38	55	0	m	A. Dixon pers. comm.

* combined EPP from 2 experimental groups

m = monogamous, pa = polyandrous, pt = polyterritorially polygynous, pm = monoterritorially polygynous, c = colonial

Table 2.1. Frequencies of extra-pair paternity (EPP) and intra-specific brood parasitism (IBP) found in field studies using DNA fingerprinting. The mating system of the DNA fingerprinted population is indicated.

2.2. Methods

2.2.1. DNA fingerprinting

Techniques for DNA fingerprinting in birds have been well described elsewhere (Burke and Bruford 1987; Burke *et al.* 1989; Birkhead *et al.* 1990; Hanotte 1991; Bruford *et al.* in press) and so only a brief summary is needed here.

2.2.2. Blood collection

Approximately 20 - 150 μ l of blood was taken by brachial venipuncture and immediately placed in at least four volumes of 1 x SSC, 10mM EDTA blood buffer (0.15 M NaCl, 15 mM trisodium citrate, 10mM EDTA, pH 7.0, autoclaved) in labelled, screw-top, 1.5 ml tubes. Adults and chicks were treated in a similar way, although chicks were occasionally sampled from the leg vein. Blood sampling by this technique has been shown to have no ill effects on birds (Stangel 1986) and no ill effects were noticed during this study.

Samples were stored at 4°C for up to two months on North Uist, then were transferred to a -70°C freezer in Leicester.

2.2.3. DNA extraction from blood

A volume of blood solution containing approximately 10 - 30 μ l of blood was suspended in 400 μ l 0.1 M Tris - Cl pH 8.0, 0.1 M NaCl, 1mM EDTA, 0.5% SDS, then incubated for 3 hours at 55°C or overnight at 37°C with 3 - 5 units ml⁻¹ proteinase K (Sigma). This was followed by two phenol/chloroform and one iso-amyl alcohol/chloroform extractions and precipitation of the DNA in 100% ethanol. The DNA was then washed in 70% ethanol and completely dried at room temperature before being dissolved in 0.5 ml 1 x TE (10 mM Tris, 1 mM EDTA, pH 7.6).

2.2.4. DNA digestion and electrophoresis

5 μ g DNA was digested with 15 units of *Alu* I restriction enzyme, used as instructed by the manufacturer, then extracted with phenol/chloroform, followed by precipitation in 100% ethanol, washing in 70% ethanol and air drying at room temperature. Digested DNA was dissolved in double-distilled water.

Electrophoresis was carried out in 1% agarose (Sigma, Type I) in a TBE buffer (0.089 M Tris, 0.089 M Borate, 2 mM EDTA, 0.5 μ g/ml ethidium bromide, pH 8.8) at 50 - 80 V for 50 - 60 hours until fragments of 2kb had migrated 28 cm. Samples were balanced for equal amounts of DNA, prior to loading on the gel, using a DNA fluorometer (Hoeffer). Each sample in loading buffer included 4.5 - 5.0 μ g digested DNA and 5 μ g ethidium bromide.

After electrophoresis, gels were washed in 0.25 M HCl twice for 7.5 min, 0.5 M

NaOH, 1.0 M NaCl twice for 15 min and finally 1 M Tris, 3 M NaCl pH 7.4 twice for 15 min. Gels were then capillary blotted in 20 x SSC onto Hybond - Nfp (Amersham) nylon membranes, for at least 3 hours or overnight. After blotting, membranes were washed briefly in 3 x SSC then fixed with UV light on a 254 nm transilluminator.

2.2.5. Probing filters

Jeffreys 33.6 probe was used, labelled with ^{32}P by primer extension from single stranded M13 vectors (Jeffreys *et al.* 1985a, b). Filters were prehybridized at 65°C for 3 hours in 0.5 M Na phosphate, 1 mM EDTA, 7% SDS and 1% bovine serum albumin, pH 7.2. Hybridization was carried out in the same solution for 16 hours at 65°C, then the filters were washed once in 0.5 M Na phosphate, 1% SDS, once in 2 x SSC, 0.1% SDS then several times in 1 x SSC, 0.1% SDS at 65°C until background levels of radiation were negligible, as measured against a blank control. Filters were then exposed against X-ray film (Fuji RX or Amersham MP) for 3 - 14 days at -70°C, either with one, two or no intensifying screens, depending on the intensity of the radiation on the filters.

2.2.6. Fingerprint analysis

Where the parental blood sample was available, all offspring were run on the same gels as their putative parents. This avoided the problem of trying to compare fingerprints between gels.

Bands between 23 and 4.4 kb were scored, as these had the clearest resolution and highest diversity on the fingerprints. Bands were scored as the same when their centres were within 0.5 mm of each other and they did not differ in intensity by at least two-fold. Band sharing coefficients were calculated as described in Wetton *et al.* 1987, by the equation 2.1:-

$$X_{ab} = \frac{2 n_{ab}}{n_a + n_b} \quad (2.1)$$

where X_{ab} is the band sharing coefficient between two individuals (a and b), n_{ab} is the number of shared bands and n_a and n_b are the number of scored bands in individuals a and b respectively. Background band sharing was calculated from 17 apparently unrelated individuals run in adjacent, or next to adjacent, tracks on a gel. Band sharing coefficients were calculated for all pair-wise comparisons between all offspring and both parents (if available). On average, 50% of offspring bands are inherited from each parent (Jeffreys *et al.* 1985a, b; Burke and Bruford 1987; Birkhead *et al.* 1990) and so, as some bands will be apparently be shared by the parents and some parental bands may be homozygous, the band sharing coefficients for first order relatives (parent-offspring and sibling-sibling)

should be greater than 0.5. Unrelated individuals should approximately show the background level of band sharing. Pair-wise band sharing coefficients should, therefore, show a bimodal distribution, with unrelated individuals in one group and first order relatives in another.

When both putative parents were available, the number of mismatched bands was calculated for each offspring, i.e. the number of bands present in the offspring which were absent from both parents. Random mutation could probably account for a single mismatched band and should be expected to occur at a rate of 1 in every 100 - 300 bands (Jeffreys *et al.* 1985a, b; Burke and Bruford 1987; Westneat 1990). Mismatches above this level are, therefore, more likely to be due to individuals not being directly related, rather than to multiple mutations.

One approach to parentage analysis compares observed and expected degrees of band sharing under the assumption that the bands in the fingerprint are inherited independently of one another and are not linked. This assumption can be tested by a segregation analysis of a large family of typically 10 or more offspring (Jeffreys *et al.* 1985a, b; Fowler *et al.* 1988; Burke *et al.* 1989; Birkhead *et al.* 1990). Families this large were not available, however, though it appeared that bands between 23 and 4.4 kb were not linked and were generally heterozygous. An alternative approach is to compare the band sharing values between individuals whose relationship is being tested with the distributions of values obtained empirically from comparisons between individuals of known, or deduced, relationship. DNA fingerprint analysis using band sharing coefficients in this way has been successfully applied by others using similar assumptions (Wetton *et al.* 1987; Westneat 1990; Lifjeld *et al.* 1991; Hanotte 1991; Hunter *et al.* in press).

2.2.7. Observed male reproductive success

Observed male reproductive success was calculated from fledging successes of individual nests found on male territories and assumes full paternity of offspring to the male occupying that territory. Methods are described in more detail in chapters 1 and 3. Only unpaired, monogamous and bigamous males are compared in this analysis, as there were only three males which were trigamous. The distribution of females amongst males was compared against a Poisson distribution calculated from equation 2.2 (from Brown and Downhower 1988):

$$\text{Poisson (random) distribution} = \sum_{n=0}^i (e^{-x})(x^n)/n! \quad (2.2)$$

where 'x' is the mean number of females per male and 'i' is the number of females.

2.3. Results

2.3.1. Observed male reproductive success

Despite an annual sex ratio of approximately 1 : 1 in both years (27 males : 25 females, 1989; 24 males : 26 females, 1990), females were not equally distributed amongst males. Fig. 2.1 shows the frequency distribution of males which had 0 - 3 females nesting on their territories. In both years the distribution of females amongst males was not significantly different from a Poisson (random) distribution (1989: $\chi^2 = 4.99$, $df = 2$, $p > 0.05$; 1990: $\chi^2 = 0.566$, $df = 3$, $p > 0.5$). The most common pairing situation overall was monogamy (41.2%) followed by bigamy (27.5%), unpaired (23.5%) and trigamy (5.9%). No male had more than three females nesting on his territory in any one year.

For observed reproductive success, unpaired males were assumed to have fathered no offspring during the breeding season, as no nests were built on their territories. The absolute number of fledglings produced per territory per breeding season varied with male status, and was significantly greater for bigamous males over monogamous males and monogamous males over unpaired males (Kruskal-Wallis ANOVA, $H = 28.5$, $df = 2$, $p < 0.001$; Fig. 2.2).

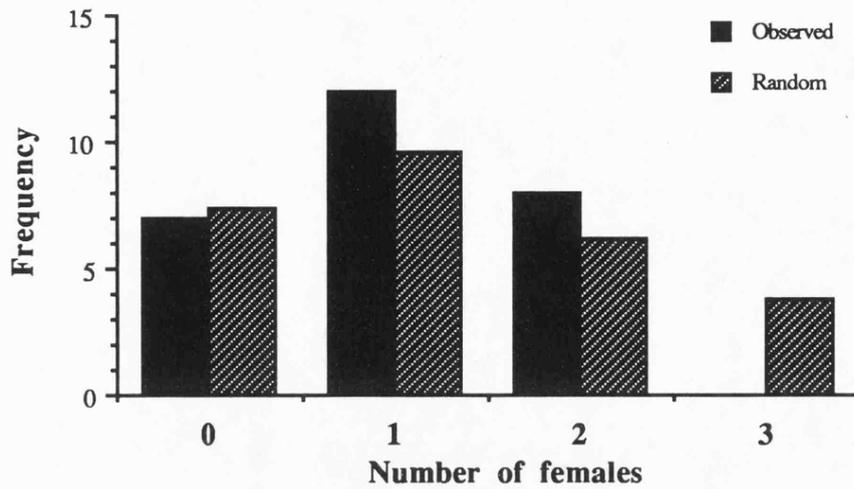
Bigamous males gained an average of 0.65 more fledglings per nesting female than monogamous males, but this difference was not significant (Mann-Whitney, $z = 1.43$, $p < 0.2$; Fig. 2.3).

2.3.2. Actual reproductive success

A total of 56 scorable DNA fingerprints were obtained for 38 offspring (from 13 families) where both parents were available, 12 offspring (from 3 families) where only the female was available and 6 offspring (from 2 families) where only the male was available. Fingerprints were also scored for a further 12 offspring (from 3 broods) which had neither parent available. Overall, seven broods of monogamous females were analysed, four of primary females, six of secondary females and one of a tertiary female; so a representative sample of broods from each nest category was available. An example of a set of fingerprints for a family which included both parents and the chicks is shown in Fig. 2.4. Where both parents were available, only two chicks, from a family of two, had more than one mismatched band. Single mismatches occurred in 4 offspring (10.5% of those for which both parents were available), giving a band mutation rate of 1 in 121; a comparable rate to that expected from the mutation of 1 band in 100 - 300 (Jeffreys *et al.* 1985a, b; Burke and Bruford 1987; Westneat 1990).

Band sharing coefficients for nestlings which could be compared to both putative parents, and which could therefore be included or excluded on the basis of multiple band mismatches, were 0.531 ± 0.131 (s.d.) for male : offspring and 0.560 ± 0.127 (s.d.) for female : offspring ($n = 36$ offspring). There was a significant negative correlation between

a) 1989



a) 1990

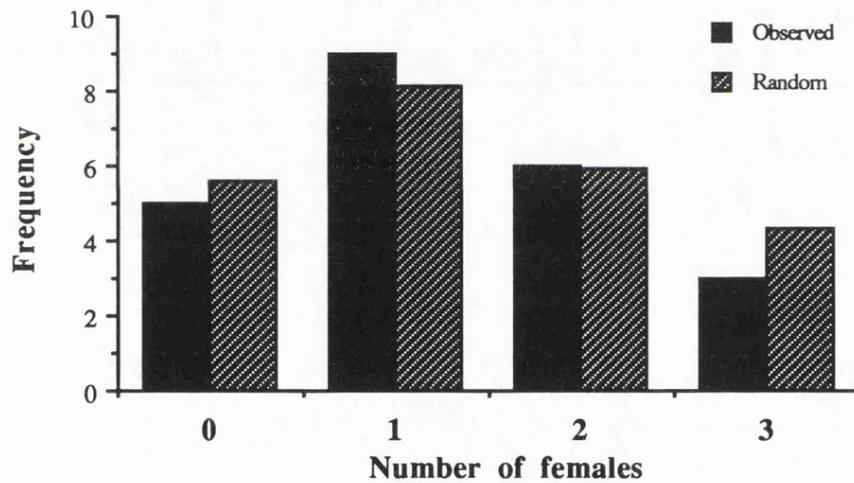


Fig. 2.1. Frequency distribution of males by pairing with different numbers of females for a) 1989 ($n = 27$) and b) 1990 ($n = 24$). The status of one male was not determined in 1990. The expected distribution of females due to them being randomly (Poisson) distributed amongst males is also shown for each year. In neither year was the observed distribution significantly different from random (1989: $\chi^2 = 4.99$, $df = 2$, $p > 0.05$; 1990: $\chi^2 = 0.566$, $df = 3$, $p > 0.5$)

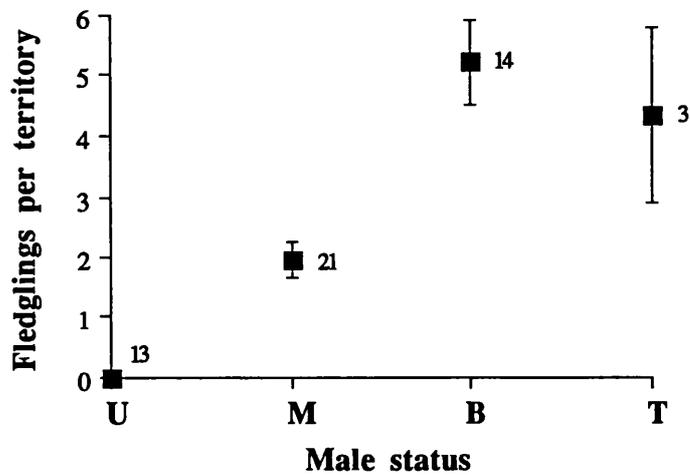


Fig. 2.2. Number of fledglings produced per territory against male pairing status (mean \pm s.e., n) (U = unpaired, M = monogamous, B = bigamous, T = trigamous). The differences are significant overall (Kruskal-Wallis ANOVA; $H = 28.5$, $df = 2$, $p < 0.001$) and between each pair-wise comparison (Mann-Whitney tests; U vs M, $z = 4.03$, $p < 0.0001$; U vs B, $z = 4.43$, $p < 0.0001$; M vs B, $z = 3.46$, $p < 0.001$). Trigamous males were omitted due to the small sample size.

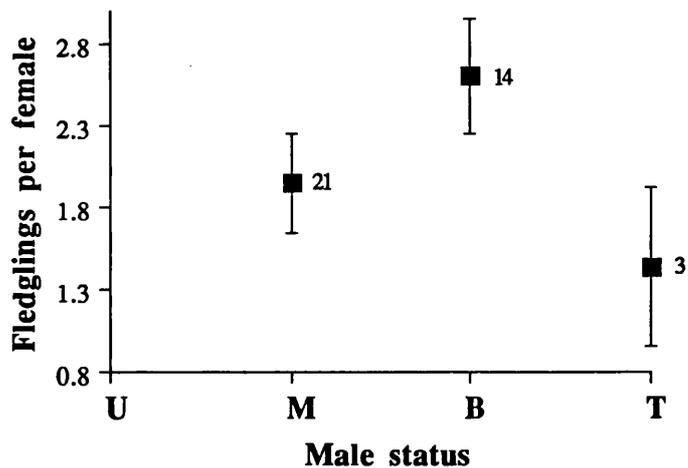


Fig. 2.3. Number of fledglings produced per female against male pairing status (mean \pm s.e., n) (U = unpaired, M = monogamous, B = bigamous, T = trigamous). There was no significant difference between M and B (Mann-Whitney test; $z = 1.43$, $p = 0.153$). Trigamous males were omitted due to the small sample size.

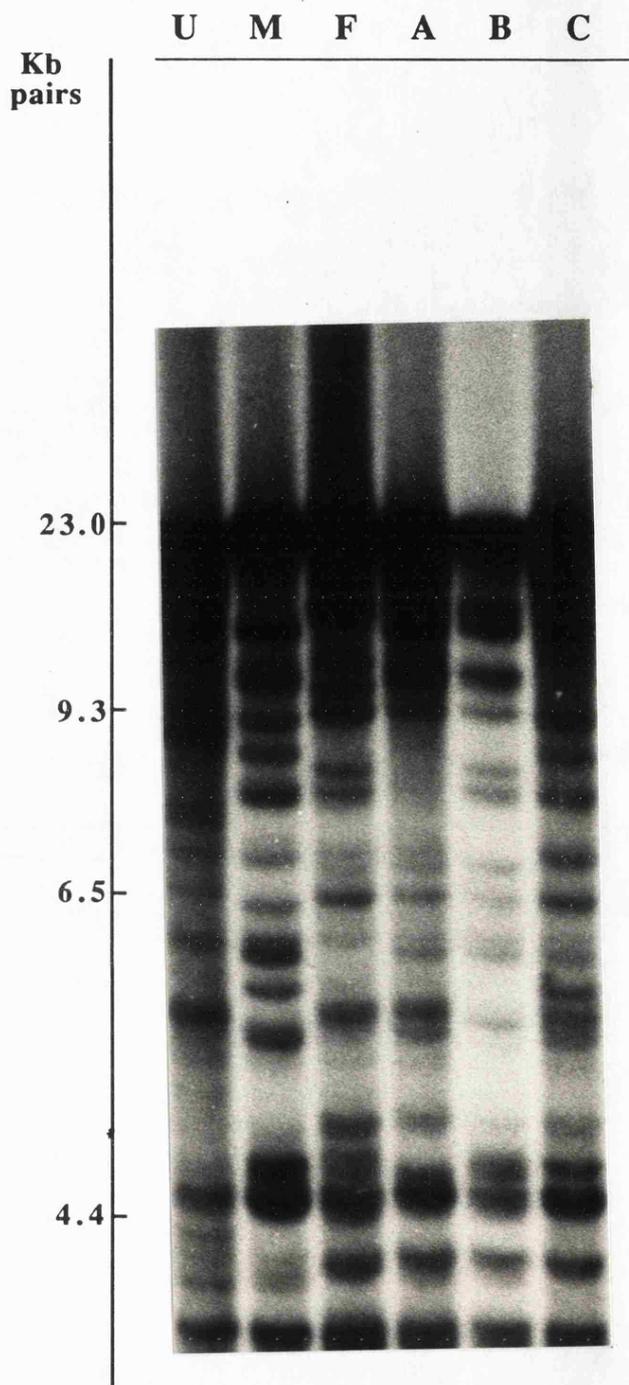


Fig. 2.4. An example of a fingerprint for a family of three offspring and both parents. The three nestlings (A, B and C), were assigned as the true, genetic offspring of both the male (M) and female (F) because all bands present in any offspring were also present in one or both parents. An unrelated corn bunting (U) is included for comparison. All fingerprints were run on the same gel.

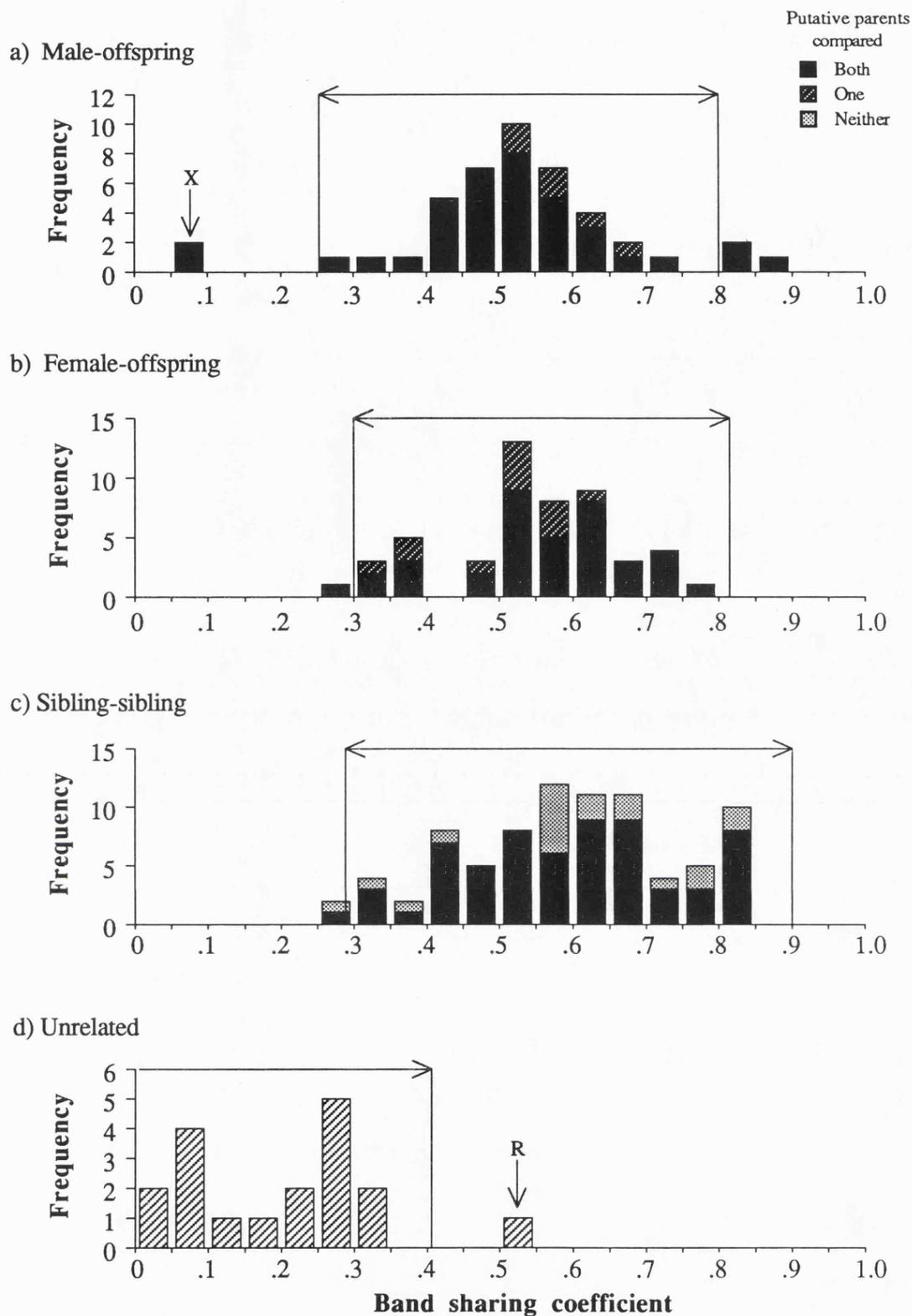


Fig. 2.5. Frequency distributions of band sharing coefficients between a) males and their offspring, b) females and their offspring, c) siblings within broods and d) apparently unrelated individuals. Offspring which were DNA fingerprinted against both putative parents are shown separately from those tested against only the male (a), female (b) or neither parent (c). Vertical lines are the 95% confidence limits of the band sharing ranges (mean \pm t x s.d.) calculated only from chicks where both parents were available for comparison (a-c). In a) the two offspring marked 'X' are not the true, genetic offspring of the father they were compared against. In both b) and c) all pairwise band sharing proportions were consistent with full first order relatedness (i.e., female-offspring and sibling-sibling). In d) the individuals with band sharing labelled 'R', are most probably not unrelated and the confidence limits for d) do not include this coefficient.

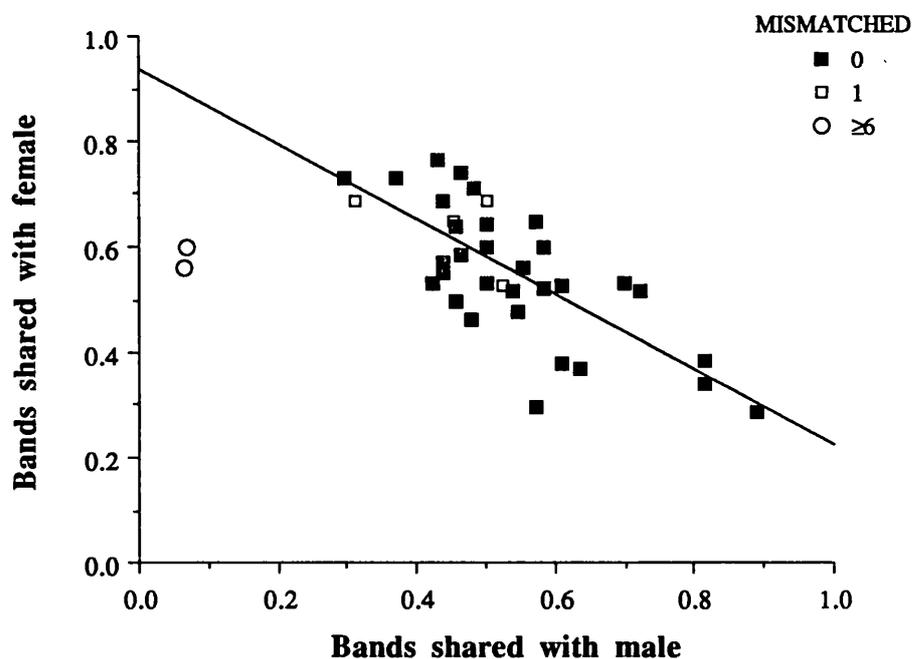


Fig. 2.6. Scattergram of parental band sharing coefficients for offspring which were DNA fingerprinted against both parents. The equation of the line was calculated from those offspring with no mismatched bands using linear regression. $Y = -0.71 X + 0.94$, $r = 0.727$, $n = 32$, $p < 0.01$. Filled squares represent 32 offspring for which all bands in the offspring could be accounted for in either parent (no mismatches), empty squares represent 4 offspring which showed one mismatched band and empty circles represent 2 offspring with more than 5 mismatched bands.

The offspring with single mismatched bands were assigned as true offspring of both parents and the offspring with several mismatched bands were assigned as the true offspring of the female but not of the male.

paternal band sharing coefficients and maternal band sharing coefficients ($r = -0.727$, $n = 32$, $p < 0.001$; Fig. 2.6), indicating that relatively low band sharing in one parent could be accounted for by correspondingly higher band sharing in the other, and was attributable to chance band transmission around the 50% level. The band sharing coefficients, from families with both parents correctly assigned, were used to determine parentage mismatches for families with only one parent available. Fig. 2.5 shows the frequency distribution of band sharing between nestlings and their putative fathers, mothers and siblings.

Band sharing coefficients for apparently unrelated birds were calculated as 0.179 ± 0.109 (s.d., $n = 17$) (Fig. 2.5). This does not include one pair-wise comparison which gave a band sharing coefficient of 0.500, which most likely represents two related individuals. Both sexes are philopatric to their natal area, and with the relatively small population on the study site, a pair of related individuals should not be unexpected.

Where both parents were available for testing, only 2 offspring (5.3%, $n = 38$) from one family had with more than one band which was not in either parent (actually six and eight bands). These offspring are shown in Fig. 2.6, and it can be seen that they are outside the range of expected band sharing coefficients for the male, but not the female, indicating that these offspring were fathered by a male other than that tested.

For families with only one parent available for testing, mean band sharing coefficients were 0.590 ± 0.058 (s.d., $n = 6$) for male : offspring and 0.500 ± 0.097 (s.d., $n = 12$) for female : offspring. Each parent-offspring combination was within the 95% confidence limits expected for full offspring-parent relatedness. For male : offspring combinations, where only the putative father was available for fingerprinting, it was concluded that there was no EPP, as siblings had band sharing coefficients within the range expected for full siblings (0.292 - 0.904; calculated from mean $\pm [t \times \text{s.d.}]$ for known siblings where both parents were available for testing and were the true parents [$n = 36$]) and so most probably shared the same mother as well. For female : offspring combinations, where only the putative mother was available for fingerprinting, there was no IBP, and although EPP cannot be ruled out in these cases, the siblings within these broods had band sharing coefficients within the range expected for full siblings and so probably shared the same father within broods. There was some overlap between the 95% confidence ranges for close relatives and non-relatives. In particular, this applies to three of the female-offspring comparisons where no male was sampled (Fig. 2.5b). There is, however, no tendency for the offspring tested against just a single parent to have low band sharing coefficients, so it seems reasonable to treat these cases as inclusions.

The conclusion is that EPP by EPC was low (4.5% of 44 offspring, or in 6.7% of 15 broods, where at least the putative male was available for fingerprinting; 95% confidence range: 0.56 - 15.06% offspring) and that IBP was absent from those offspring tested against the putative mother (0% of 50 offspring, or in 0% of 16 broods, where at least the

putative mother was available for fingerprinting; 95% confidence range: 0.00 - 5.82% offspring). No multiple parentage was recorded in any brood (0% of 21 broods where at least one putative parent was available; 95% confidence range: 0.00 - 13.25%). The upper and lower 95% confidence limits for these percentages were obtained from Rohlf and Sokal (1981).

2.4. Discussion

2.4.1. DNA fingerprinting analysis

A potential problem with assigning parentage using band sharing coefficients is that they do not correspond directly to 'relatedness' in the Hamilton sense (Hamilton 1964). Some bands will simply be shared by chance between individuals within populations and some will be shared as a result of individuals being related. In small populations where both sexes are philopatric (as in this study population, *M. Shepherd* pers. comm.), inbreeding could occur by chance and so the band sharing would effectively be increased between individuals. The occasionally high band sharing coefficients between individuals of known relatedness (in this case offspring : parent and sibling : sibling) could reflect a certain amount of inbreeding within the population.

A potential statistical problem with comparing band sharing between siblings is how many pair-wise comparisons to use. In this analysis I used all pair-wise comparisons within broods to obtain the 95% confidence limits, but some of these will be non-independent and so only limited reliance can be placed on the sibling - sibling band sharing coefficients when no parents were available. As most of the results presented here depended on multiple mismatched bands to exclude paternity, or band sharing where one parent was available, the problem was not a major one. A second potential problem is quasi-brood parasitism, where a female dumps an egg in a nest of another female which is paired with the male which fertilized the dumped egg. This is probably a rare event (Birkhead *et al.* 1990) in monogamous species because the chances of a male having a successful EPC with a female, which then dumps the egg into his own nest, are probably low. In polygyny these chances may be increased, however, because several females which are being fertilized by the same male are also nesting on the same territory, so the opportunities for quasi-IBP may be greater. This type of quasi-brood parasitism would be detected if both parents were available for fingerprinting, but if only the male was available band sharing coefficients would probably not detect the difference between half-siblings and full-siblings. This is because the ranges of band sharing coefficients between half-siblings and full-siblings will be greatly overlapping, making it impossible to separate the band sharing coefficients of half-siblings. In this study, quasi-IBP was not found in broods where both parents were available for fingerprinting, nor was egg dumping observed in the field (chapter 3).

Further work on the genetic structure of geographically isolated, philopatric species may reveal more about mechanisms of inbreeding avoidance or show that chance is the main factor involved in individuals avoiding breeding with close relatives. A useful extension of DNA fingerprinting would be to use band sharing coefficients to estimate relatedness (e.g., Jones *et al.* 1991).

2.4.2. Extra-pair paternity

Extra-pair parentage occurred at a low level in the corn bunting population in this study, so observed reproductive output of nests will reliably reveal the reproductive success of both parents.

Extra-pair paternity occurred in only one brood (both chicks in a brood of two) and could have arisen by several means. Either this was a genuine case of EPP or of the male fertilizing the female after having changed rapidly (either because the territorial male changed or the female switched territories), or else the male was incorrectly assigned to the nest in question, or the blood samples of the offspring or male were mixed up. Initially, one other case of apparent EPP was assigned to a full brood of two, but this turned out to be a mistake with a ring combination; when corrected it was found that the pair male was indeed the real father of the offspring. In another case of a brood of five offspring, two pairs of offspring had identical fingerprints, which is almost certainly an impossibility for birds hatching from separate eggs, so they must have been the same individual. When these were re-run using blood collected on the same day for all but one of the offspring, it was evident that blood tubes had been mislabelled in the field on this occasion. So, although these mistakes were rectified, the case of EPP in the one brood could not be double-checked because of technical difficulties. Rapid mate switching (e.g, Zenone *et al.* 1979; Quinn *et al.* 1987) was an unlikely explanation because the territory holding male did not change and although the female was unringed at the time of laying, and may have visited other males' territories prior to settling, she had definitely not previously attempted to breed that season. It must, therefore, remain unresolved for the moment, although this would not change the general conclusion that both EPP and IBP occurred at a very low rate in this study population.

The high security of paternity by male corn buntings could be explained by the following:-

- 1) The observed pair copulation rate was very low, with less than 10 recorded, casually and during other watches, over two years (pers. obs.). Other workers have reported similar low copulation rates for the corn bunting, both in this study population (M. Shepherd pers. comm.) and others (Denmark, A.P. Møller pers. comm.; Liverpool, U.K., D.B.A. Thompson pers. comm.; Switzerland, J. Hegelbach pers. comm.). Copulations were possibly not seen because they were hidden, but the study site was open,

with no dense vegetation, especially early in the season, and those copulations that were seen were out in the open, often easily observed and accompanied by a distinctive female mating call. It is, therefore, more likely that the copulation rate was genuinely low, rather than just under-recorded.

Low rates of copulation are associated with species in which males guard their females against other males during the fertile period (review in Birkhead *et al.* 1987), and although data on mate guarding in corn buntings are not yet available (D. Currie in prep.), early indications suggest that males are closely associated with their females prior to egg laying. On two occasions when females were trapped and were, therefore, temporarily absent, when they were subsequently released back onto male territories (one during incubation and one during the nestling period) the territory holding male immediately chased the female to the ground and forced copulation. This suggests that sperm competition may at least play some role in the evolution of corn bunting reproductive behaviour.

Promiscuous behaviour, whereby females copulate with several males prior to laying (e.g., red-winged blackbirds, Gibbs *et al.* 1990) did not occur in the corn buntings in this study, despite previous suggestions that this species was promiscuous (Hegelbach and Ziswiler 1979; Møller 1983; Hegelbach 1984).

2) Male corn buntings are territorial and floating males (i.e., non-territorial, mobile males which intrude from territory to territory) only rarely occurred (once in two years, for one day only). Unpaired males defended territories, all males rarely trespass into other males' territories and when they do, they are neighbours (M. Shepherd pers. comm.). The lack of intruding males suggests that searching for EPCs by acting as a sneaky male may not be a profitable tactic in this species, possibly because the risk, to a sneak, of losing a territory is too great or male aggression makes intrusion dangerous. The openness and high visibility of the habitat means that not only are intruding males relatively easy to see, but their empty territory would be seen to be undefended as well. Unpaired males may stand a better chance of obtaining matings if they hold a territory in the hope of a female settling. Male intrusion rates have been found to be relatively high in species for which EPP has been recorded using DNA fingerprinting (e.g., indigo buntings [Westneat 1987a, b, 1990]; reed buntings [S. O'Malley and A. Dixon pers. comm.]). Westneat (1987b) found that non-territorial, floating males (usually in their first year) were not the main culprits in intrusions but that already paired, territorial males were. Westneat (1987b, 1988) showed that floaters spent more time singing to try to obtain a territory than searching for EPCs, suggesting that on the whole holding a territory is the best option for a male which is trying to reproduce.

3) Female corn buntings on a territory tended to breed asynchronously and this could have allowed polygynous males to mate guard all his females successfully. Synchrony of female breeding has been suggested as a female guard against EPCs in monogamous

species (Birkhead and Biggins 1987), yet within polygynous species, synchrony within a male's harem could potentially be costly for both sexes (chapter 6). Costs to synchronous breeding for two females nesting on the same territory could include suffering from unwanted EPC attempts by other males and sharing a male's paternal effort when they both need it most. For a species where there is no cost to breeding later in the season, as in corn buntings (chapter 3), the best option may be to delay nesting until the overlap between broods became unimportant in reducing male benefits. Males could also benefit from asynchronous breeding within his harem, as it means he could effectively guard both females and spread his paternal care load. Temporal spacing of nests is discussed further in chapter 6.

2.4.3. Intra-specific brood parasitism

Intra-specific brood parasitism was not recorded in this study by DNA fingerprinting or by observation of clutches as they were laid (chapter 3). Eggs of individual females were distinctively shaped and background-coloured, no female appeared to lay two eggs in one day and eggs were numbered with an indelible marker as they were laid, and so the removal of an egg, and replacement by a cuckold's egg, would have been noticed.

Of those species tested to date, DNA fingerprinting has shown that IBP is less frequent than EPP across species, and has been recorded in only two species, zebra finches (Birkhead *et al.* 1990) and purple martins (Morton *et al.* 1990)(Table 2.1), although nest observations have shown IBP to occur in other species (e.g., cliff swallow [Brown 1984]; moorhen [Gibbons 1986]; starling [Evans 1988; Pinxten *et al.* 1991]; barn swallow [Møller 1989]).

Egg dumping could occur either deliberately, by a female parasitizing another's nest, or accidentally, by a female laying an egg in another's nest which she thinks is her own (Andersson 1984; Evans 1988). Accidental egg dumping is only likely to occur in colonial species and so egg dumping in corn buntings would be unlikely to occur in this way. Corn bunting nests are not at all conspicuous, as some zebra finch nests are (Birkhead *et al.* 1990), but there is no evidence to suggest that hidden nests are more or less vulnerable to IBP; after all, meadow pipits and reed warblers both have cryptic or concealed nests, yet cuckoos regularly use them as hosts to raise their young (Glue and Morgan 1972; Brooke and Davies 1987).

Corn bunting eggs are marked with dark streaks and blobs, and both background colour and shape appear more variable between females than within clutches, as has been shown in other species (e.g., Gibbons 1986; Thomas *et al.* 1989). It has been suggested that individual female egg variation may act as a reference marker for females to distinguish foreign eggs of intraspecific hosts (Petrie and Møller 1991), although data in support of this hypothesis are currently lacking. Furthermore, there is good evidence from studies of

inter-specific brood parasitism, between cuckoos and their hosts, which does not support the theory that egg patterns have evolved as a defence against brood parasitism (Davies and Brooke 1989a, b). No experiments were conducted to test if female corn buntings could distinguish and remove eggs added to their clutches.

Yom-Tov (1980) suggested that nesting synchrony within a breeding population may decrease the likelihood of brood parasitism by swamping nest parasites with available nests for a very short period, as could occur in starlings in which 80% of females lay within 5 days of each other (Dunnet 1955). The evidence to support this argument is very weak. Yom-Tov (1980) observed that there were more species which were inter-specific nest parasites in areas where birds generally had protracted breeding seasons, such as the tropics, but no allowance was made for the greater niche diversity which arises for parasites when there are more species to use. This observation probably reflects the fact that there are generally more species of all types in tropical areas than near the poles.

An alternative theory is that population nesting synchrony is not caused by the necessity to avoid IBP, but to avoid EPC attempts by males (Birkhead and Biggins 1987), or it may arise due to environmental factors, such as day length, ambient temperature or food supply. Population nesting synchrony could even increase the possibilities of suffering IBP, because there is evidence to suggest that females who parasitize conspecifics' nests are those females which have recently lost clutches they were laying themselves (e.g., ruddy duck, referred to in Yom-Tov 1980), so in a population of synchronous nesters, females which lose their nests during laying have a ready supply of hosts, all at the best stage (laying) for parasitizing.

In corn buntings, the rate of IBP may be expected to be very low as most IBP occurs in hole-nesting species (e.g., starlings [Evans 1988; Pinxten *et al.* 1991]), colonial nesting species (e.g., swallow species [Brown 1984; Møller 1989; Morton *et al.* 1990]) or species with a floating population of apparently non-breeding, young females (e.g., ducks [refs. in Yom-Tov 1980]). Nest sites are possibly not as limiting for corn buntings as they are for hole nesting species; all females breed and the opportunities for IBP provided by colonial nesting do not exist.

Evidence regarding the success of IBP as an alternative and successful reproductive strategy, rather than making the best of a bad job (e.g., nest loss during laying), are not well documented but reports so far suggest that dumped eggs are not as successful as the host eggs, often because they are added to the host clutch during incubation, and are subsequently not incubated when the host brood hatches (Gibbons 1986), or they hatch late and cannot compete for food successfully against the older cohabitants of the nest (Petrie and Møller 1991). As part of a mixed reproductive strategy, however, IBP may increase a pair's reproductive success if the female has the opportunity to egg dump during the host's laying period, as found in the colonial white-fronted bee-eater (Emlen and Wrege 1986).

2.4.4. Male reproductive success

From the DNA fingerprinting results, it appears that polygynous males do indeed have a higher annual reproductive success than monogamous and unpaired males. Bigamous males fathered 0.6 more fledglings, per female nesting on the territory, than monogamous males and although this was not a significant difference, it does support the data presented in chapter 3, which shows that nests of monogamous females have a lower fledging success than nests of polygynously paired females.

Males which remained unpaired were at a disadvantage to those which were polygynous because males without females had no reproductive success. The distribution of females among males was not significantly different from a Poisson (random) distribution in both years, showing that the majority of females were not monopolized by only a few males and suggesting that the majority of resources could not be monopolized by a minority of males. The observed distribution of females among males was consistent with a pattern of random settlement for females (Sutherland 1985), which is discussed further in relation to polygyny in chapter 6.

2.5. Summary

1) Despite a sex ratio approximating to unity, female corn buntings were not equally distributed amongst males. In 1989 and 1990, 41.2% of males were monogamously paired, 29.4% were polygynous and 23.5% remained unpaired. Polygynous males usually paired with two females, although in 1990 three males were trigamous. In both years, the distribution of females among males was not significantly different from random.

2) Polygynous males fledged more offspring from their territories than did monogamous males, mainly because they had more females. The fledging success per nesting female was slightly higher in territories of polygynous males, but not significantly so. Territories of unpaired males fledged no offspring.

3) DNA fingerprinting was used to determine both the true paternity of 44 offspring from 15 families and the true maternity from 50 offspring from 16 families. A further 12 offspring from 3 broods for which neither putative parent was available were also fingerprinted. Actual reproductive success of parents was very close to the observed reproductive success. There were only 2 possible cases of EPP due to EPC (4.5% of offspring, or in 6.7% of broods), both from the same brood. There were no cases of IBP (0% of offspring, or 0% in 16 broods).

4) Copulation rate was low and EPP was probably low because of mate guarding by the male, asynchrony between broods for polygynous males and low intrusion rates due to the poor chances of sneaking onto a neighbour's territory undetected and the costs of leaving a territory unguarded.

5) IBP was not recorded, probably because the opportunities for IBP were low in corn buntings because nests were both temporally and spacially dispersed.

Chapter 3. Polygyny and female reproductive success

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3.4.5. Female reproductive success in relation to the mating system

3.5. Summary

3.1. Introduction

There are potential costs and benefits for females when pairing polygynously. Costs could include sharing resources such as available food or male parental care (Drycz 1977; Patterson *et al.* 1980; Alatalo *et al.* 1981, 1982; Yasukawa and Searcy 1982; Catchpole *et al.* 1985; Muldal *et al.* 1986; Stenmark *et al.* 1988; Lifjeld and Slagsvold 1989). Benefits could include group nest defence (e.g., Woolfenden and Fitzpatrick 1984; Picman *et al.* 1988) or enhanced foraging of individuals in groups (Ward and Zahavi 1973; but see Mock *et al.* 1988). In most polygynous, passerine species, females have a lower reproductive success if they pair with already paired males than they would if they paired monogamously, probably as a result of one or more factors:-

1) Later egg laying date: In some species reproductive success per nesting attempt declines as the season progresses, possibly because of environmental effects such as food depletion, or because of female quality, such that older, more experienced or higher quality females breed earlier, or because territories taken up later in the season are of lower quality than those taken earlier (e.g., Perrins 1965; Lack 1966; Alatalo and Lundberg 1984; Newton and Marquiss 1984).

2) Reduced male nuptial feeds: Nuptial feeding may be a valuable source of food for females preparing to lay as it can increase clutch size or advance laying date (Lifjeld and Slagsvold 1986). Incubation feeding of female pied flycatchers by the male has been shown to maintain female body condition and, therefore, enhance reproductive success

(Lifjeld *et al.* 1987). In pied flycatchers, females paired to polygynous males received fewer incubation feeds than did monogamously paired females and were subsequently less successful breeders (Lifjeld *et al.* 1987).

3) Reduced male parental investment: Secondary and subsequent females of polygynous males often receive less help with provisioning of nestling than monogamous females or primary females of the same males, and so suffer reduced reproductive success. This has been found, for example, in pied flycatchers (Alatalo *et al.* 1981, 1982; Stenmark *et al.* 1988; Lifjeld and Slagsvold 1989, 1990), great reed warblers (Drycz 1977, 1986; Catchpole *et al.* 1985; Urano 1990), bobolinks (Wittenberger 1980b) and red-winged blackbirds (Patterson *et al.* 1980; Yasukawa and Searcy 1982; Muldal *et al.* 1986; but see Picman *et al.* 1988).

Benefits of polygyny to females have been observed in one population of red-winged blackbirds, where secondary females of polygynously paired males were more successful than monogamous females because they acted as a group in nest defence and suffered reduced predation as a result (Picman *et al.* 1988). Similar group nest defence increases reproductive success in the cooperatively breeding Florida scrub jay (Woolfenden and Fitzpatrick 1984). Reduced predation was also a benefit for female eastern meadowlarks which paired polygynously, as polygynous males were considered to be better than monogamous males at nest defence (Knapton 1988). There is no evidence supporting, or refuting, the idea that females of polygynous males benefit from each other through enhanced foraging (as suggested for group-living birds by Ward and Zahavi 1973; but see Mock *et al.* 1988).

In some cases, polygyny may be neither costly nor beneficial, for example, weak female competition combined with a minor role for males in nest care meant that female yellow-headed blackbirds suffered no costs to mating polygynously and received no benefits either (Lightbody and Weatherhead 1987). Similarly, female dickcissels did not suffer costs to pairing polygynously as the habitat was so homogeneous that male territories did not differ significantly in quality and secondary nests were also fed by males (Zimmerman 1966).

It may be that for populations under variable ecological conditions, with fluctuating predation risks and/or food availability, the costs and benefits accruing to the females pairing polygynously also vary, with polygyny sometimes being the best option.

Breeding success in female corn buntings under different pairing options should depend on one or more of the following:-

1. Timing of breeding
2. Relative importance of the males in nestling provisioning
3. Nuptial feeding of the female by the male
4. Possible benefits from other females in nest defence

5. Habitat quality for nest site or food supply

One should expect lower reproductive success in secondary females of polygynous males, compared with primary females of those males and monogamous females, if female corn buntings compete for resources such as male nuptial and/or nestling feeds, or nesting or foraging habitat. If breeding success decreases as the season progresses, one should expect secondary females to be less successful than their corresponding primary females because secondary females, by definition, nest later.

Polygynously mated females could have a higher reproductive success than monogamous females if they benefitted from each other in nest defence or if polygynous males worked harder to feed all nestlings and/or to provide nuptial feeds for all their females. If, however, territories are of similar quality, and males play an unimportant role in nest provisioning or nuptial feeding, all nest classes might be expected to have a similar reproductive success.

This chapter describes the reproductive success of monogamous, primary and secondary female corn buntings in relation to the polygynous mating system and discusses the possible costs and benefits of polygyny for females.

3.2. Methods

Nests found at the building stage were checked every day or every second day to determine the first egg date. Eggs were numbered consecutively as they were laid using a permanent, felt-tip marker. Nests found with complete clutches were treated similarly. Only clutches which were complete and recorded before hatching were used in the clutch size analysis.

Nests with known first egg dates were revisited after 11-12 days of incubation, when they were close to hatching. Nests which were found at the incubation stage were visited or observed more regularly in order to obtain the hatching date. Hatching success was calculated from those nests which underwent a complete incubation period and/or survived to hatching. Individual chicks were marked, first with combinations of claw clippings, and from day 5 (day 1 = day of hatching), with numbered, metal rings. It was not usually possible to determine the hatching order of the eggs as most of the chicks hatched simultaneously, although this was sometimes possible for the last chick to hatch. Fledging success (number of fledglings per nest) was measured as the number of nestlings leaving the nest, by three methods:-

- 1) for all nests, including those that failed prior to hatching (overall fledging success)
- 2) for nests with at least one hatched egg
- 3) for nests which fledged at least one chick ('successful' nests).

For those nests found after clutch completion, first egg dates (FEDs) were calculated from hatching date or chick age, using the following formula:

FED = hatch date - 12 days (incubation) - clutch size + 1 day

Incubation usually began with the penultimate egg and hatch date was either known or calculated from the age of the chicks.

Eighty-three nests were examined at least once before fledging and multiple visits were made to most nests. The sample sizes in the following analyses are variable, depending on the stage at which the nests were found, as not all data were available for each nest.

The dates shown on figures were consecutively numbered for both years such that 1 = 1st May.

3.3. Results

3.3.1. Breeding success in 1989 and 1990

For first clutches, Table 3.1 shows the between-year comparisons and combined data for the mean clutch size, hatching success, overall fledging success, fledging success from nests hatching at least one egg and fledging success from successful nests. Table 3.2 shows similar results for the relay clutches. There were no significant differences between years for any breeding success parameter. As the breeding parameters for the two years were so similar, the rest of the analysis uses combined data unless otherwise stated.

3.3.2. First egg dates (FEDs), clutch sizes and fledging success

FEDs of first clutches were not significantly different between years (Mann-Whitney, $z = 1.84$, $n(1989) = 25$, $n(1990) = 20$, $p > 0.05$), although there was a trend towards earlier first clutches in 1990 by approximately 8 days. Fig. 3.1 shows the frequency distribution of first egg dates for first clutches, relays and second broods, for both years combined, with the 1989 data corrected for the difference in mean laying date (corrected FED = FED - 8 days).

There was no significant tendency for the size of first clutches to decrease or increase as the season progressed ($r_s = -0.047$, $n = 34$, $p < 0.8$; Fig 3.2). There was no significant relationship between corrected FED and the proportion of eggs hatching from first clutches which underwent full incubation ($r_s = 0.265$, $n = 28$, $p < 0.2$; Fig 3.3). There was a significant positive correlation between corrected FED and overall fledging success for all first clutch nests ($r_s = 0.418$, $n = 45$, $p < 0.01$; Fig. 3.4a). There was no significant relationship between corrected FED and the fledging success of first clutch nests that hatched, although there was a trend towards a positive correlation ($r_s = 0.314$, $n = 36$, $p < 0.1$; Fig 3.4b). There was a significant relationship between corrected FED and fledging success of successful nests ($r_s = 0.453$, $n = 23$, $p < 0.05$; Fig. 3.4c). The positive correlation between corrected FED and overall fledging success was mainly due to early nests completely failing more often than later nests, and early nests producing slightly fewer young.

	1989	1990	combined data	between-year comparison
clutch size	3.74 ± 0.65 3-5 19	3.77 ± 0.66 2-5 17	3.75 ± 0.65 2-5 36	U' = 172.5 p < 0.7
% hatching success	75.51 ± 29.50 33.3-100 49 eggs 13 clutches	91.49 ± 12.31 75-100 47 eggs 12 clutches	83.33 ± 24.26 33.3-100 96 eggs 25 clutches	χ ² = 0.232 df = 1 p < 0.7 (eggs)
overall fledging success	1.20 ± 1.41 0-5 25	1.55 ± 1.77 0-4 22	1.36 ± 1.58 0-5 47	z = 0.599 p < 0.6
fledging success of hatched nests	1.52 ± 1.40 0-4 21	2.00 ± 1.77 0-5 17	1.74 ± 1.57 0-5 38	z = 0.884 p < 0.4
fledging success of successful nests	2.46 ± 0.88 1-4 13	3.09 ± 1.14 1-5 11	2.75 ± 1.03 1-5 24	U' = 95.5 p < 0.2

Table 3.1. Between-year comparison and combined data for breeding parameters of first clutches. Numbers are mean ± s.d., range and sample size from the top downwards respectively. Between-year comparisons were made using Mann-Whitney tests or chi-square tests.

	1989	1990	combined data	between-year comparison
clutch size	4.00 ± 0.76 3-5 8	4.00 ± 0.95 2-5 12	4.00 ± 0.86 2-5 20	U' = 50 p < 0.9
% hatching success	84.00 ± 28.92 33.3-100 25 eggs 6 clutches	81.82 ± 21.91 75-100 22 eggs 5 clutches	82.98 ± 24.72 33.3-100 47 eggs 11 clutches	χ ² = 0.232 df = 1 p < 0.7 (eggs)
overall fledging success	2.20 ± 1.62 0-5 10	1.73 ± 1.83 0-4 15	1.92 ± 1.73 0-5 25	U' = 89 p < 0.5
fledging success of hatched nests	2.44 ± 1.51 0-4 9	2.89 ± 1.45 0-5 9	2.67 ± 1.46 0-5 18	U' = 40 p < 0.6
fledging success of successful nests	2.75 ± 1.28 1-4 8	3.25 ± 1.04 1-5 8	3.00 ± 1.16 1-5 16	U' = 38 p < 0.6

Table 3.2. Between-year comparison and combined data for breeding parameters of relay clutches. Numbers are means, ranges, sample sizes and standard deviations from the top downwards respectively. Between-year comparisons were made using Mann-Whitney tests or chi-square tests.

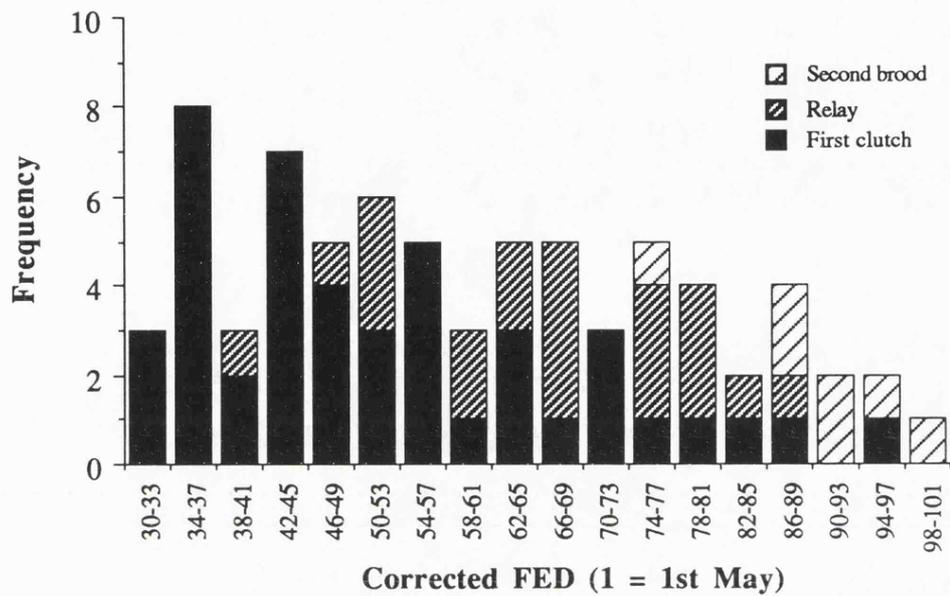


Fig. 3.1. Frequency distribution of first egg dates (FEDs) for 1989 and 1990 combined. The FEDs for 1989 have been standardized against the mean FED for 1990. First clutches, relays and second broods are shown separately.

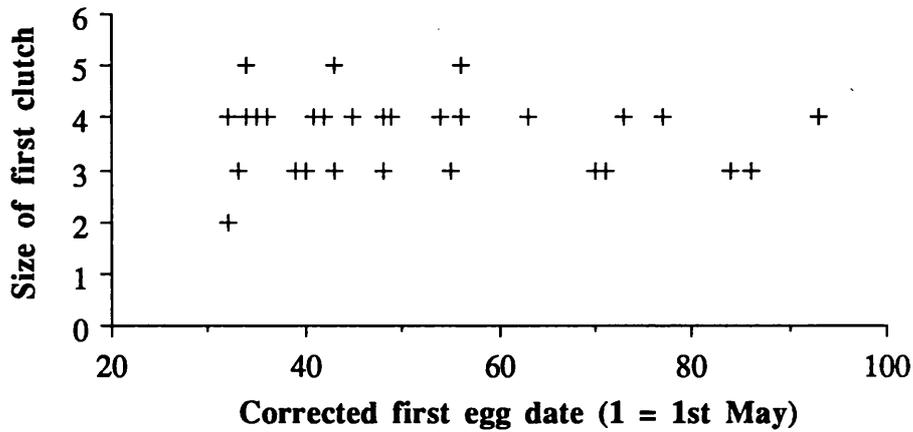


Fig. 3.2. Scatter plot of first clutch size against corrected FED. There was no significant association between the two variables ($r_s = -0.047$, $n = 34$, $p < 0.8$).

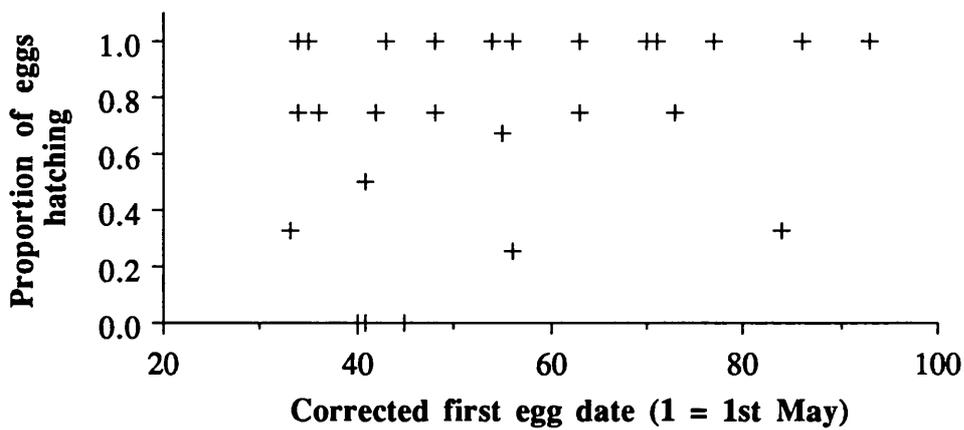
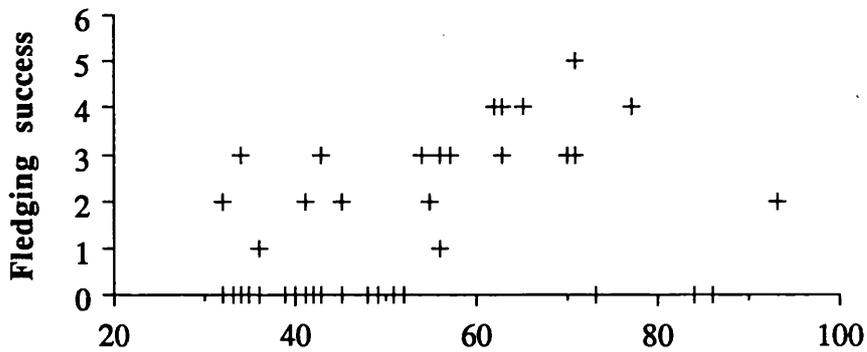
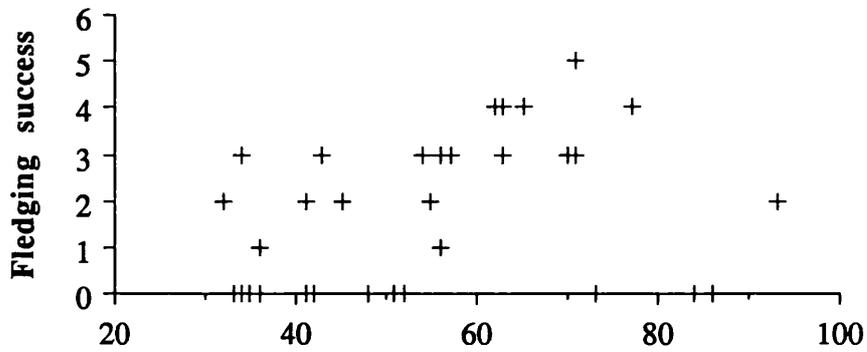


Fig. 3.3. Scatter plot of proportion of eggs hatching, in first clutches, against corrected first egg date. There was no significant association between the two variables ($r_s = 0.265$, $n = 28$, $p < 0.2$).

a) All nests



b) Hatching nests



c) Successful nests

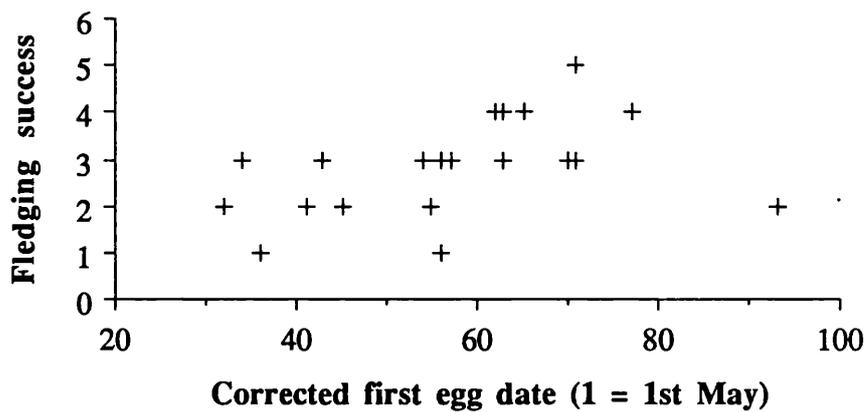


Fig. 3.4. Scatter plots of fledging success, for first clutches, against corrected FED, for a) all nests ($r_s = 0.418$, $n = 45$, $p < 0.01$), b) nests which hatched at least one egg ($r_s = 0.314$, $n = 36$, $p < 0.1$) and c) nests which were successful in fledging at least one chick ($r_s = 0.453$, $n = 23$, $p < 0.05$).

3.3.3. Second broods and relays

Only 23.3% (n = 30) of successful first broods were followed by a second breeding attempt. My definition of second broods may have over-estimated the actual occurrences if fledglings died soon after leaving the first nest (as was likely in at least some of the cases, where females were found relaying only a few days after fledging their first brood). Successful first broods which were followed by a second breeding attempt were, on average, 13.6 days earlier than successful first broods which were not. This difference was significant (Mann-Whitney, $z = 1.966$, n (with 2nd brood) = 7, n (without) = 23, $p < 0.05$).

Relays were common and 86.4% (n = 22) of females which failed with their first nests tried again. Within females, clutch sizes of relays were not significantly different from size of first clutches (Wilcoxon signed rank test, $T = 13$, $N = 6$, $p < 0.4$). There was no difference between years for the proportion of relays to first clutches ($\chi^2 = 1.096$, $df = 1$, $p < 0.3$). There were no differences between relays and first clutches for the proportions of successful nests to completely failed nests ($\chi^2 = 0.947$, $df = 1$, $p < 0.4$), so relays were not more, or less, likely to fail than first clutches. There were no differences between first clutches and relays for clutch size (Mann-Whitney, $z = 1.283$, n (1st) = 36, n (relay) = 19, $p < 0.25$), proportion of eggs hatching (Mann-Whitney, $z = 0.033$, n (1st) = 26, n (relay) = 13, $p < 0.98$) or fledging success of successful nests (Mann-Whitney, $z = 0.684$, n (1st) = 23, n (relay) = 16, $p < 0.5$). The difference between first clutches and relays for fledging success of hatched nests was of borderline significance (Mann-Whitney, $z = 1.959$, n (1st) = 36, n (relay) = 18, $p = 0.050$, relays > first clutches) but overall fledging success was not significantly different between the two nest classes (Mann-Whitney, $z = 1.397$, n (1st) = 47, n (relay) = 25, $p < 0.2$), although neither of these comparisons are based on independent samples, as each nest in the 'relay' category was bound to mean that there was a complete nest failure in the 'first clutch' category. So the correct comparison of fledging success between the first clutches and the relays is between the fledging success of successful nests (i.e., those nests fledging at least one nestling). Relays and first clutches were, therefore, not different in terms of breeding success per nest.

3.3.4. Effects of female age on reproductive success

Corn buntings breed in the first summer after hatching. Most females were first ringed while breeding and so were not of known age. Eleven females ringed between 1987 and 1989 as nestlings were subsequently found breeding on the study site and were, therefore, of known age. As sample sizes were small I used two age categories of females: known first-years (hatched in previous calendar year) and after first-years (hatched before previous calendar year). Overall fledging success was used as a measure of reproductive success. As some females owned several nests in one season (due to relays and second broods) I

compared average overall fledging success per female, between age groups. There was no significant difference between age groups (Mann-Whitney, test, $z = 1.642$, n (1st year) = 7, n (older than 1st year) = 13, $p < 0.15$).

There was no difference between monogamous and bigamous nests for female age when comparing all nests where female age category was known ($\chi^2 = 0.208$, $df = 2$, $p < 0.7$).

3.3.5. Female reproductive success in relation to the mating system

There were no significant differences in clutch size between monogamous, primary and secondary nests (Kruskal-Wallis ANOVA, $H = 5.00$, $df = 2$, $p < 0.1$; Fig. 3.5a). Hatching success was not significantly different between the groups (Kruskal-Wallis ANOVA, $H = 2.85$, $df = 2$, $p > 0.1$; Fig. 3.5b) and neither was the proportion of hatched eggs in the clutch (number hatched/clutch size; Kruskal-Wallis ANOVA, $H = 0.362$, $df = 2$, $p > 0.5$; Fig. 3.5c). Fledging success was significantly lower for monogamous nests than for either primary or secondary nests, both when including all nests (Kruskal-Wallis ANOVA, $H = 6.88$, $df = 2$, $p < 0.05$; Fig. 3.6a) and when only including nests with at least one hatched egg (Kruskal-Wallis ANOVA, $H = 7.87$, $df = 2$, $p < 0.025$; Fig. 3.6b). There were no significant differences between primary and secondary nests for median fledging success in either case (All nests, Mann-Whitney, $z = 0.188$, $p < 0.9$; hatching nests $z = 0.332$, $p < 0.8$). Fledging success for nests which fledged at least one young (i.e. successful nests) was not significantly different between the three nest classes, although the trend was for monogamous nests to fledge fewer young than bigamous nests (Kruskal-Wallis ANOVA, $H = 4.36$, $df = 2$, $p < 0.1$; Fig. 3.6c).

Monogamous and primary females were not significantly different for FED of first clutches (Mann-Whitney, $z = 0.186$, n (monogamous) = 22, n (primary) = 14, $p < 0.9$). Secondary females were, of course, later by definition.

The proportions of chicks that died, out of those hatching, were not significantly different among monogamous, primary or secondary nests (Kruskal-Wallis ANOVA, $H = 2.90$, $df = 2$, $p < 0.20$), although there was a trend towards increased mortality in monogamous nests compared to bigamous nests (Mann-Whitney, $z = 1.702$, $p < 0.09$).

There were no differences between monogamous and bigamous nests for the way in which total nest failures occurred. Monogamous and bigamous nests were equally likely to be predated or deserted/starved ($\chi^2 = 0.068$, $df = 2$, $p < 0.8$).

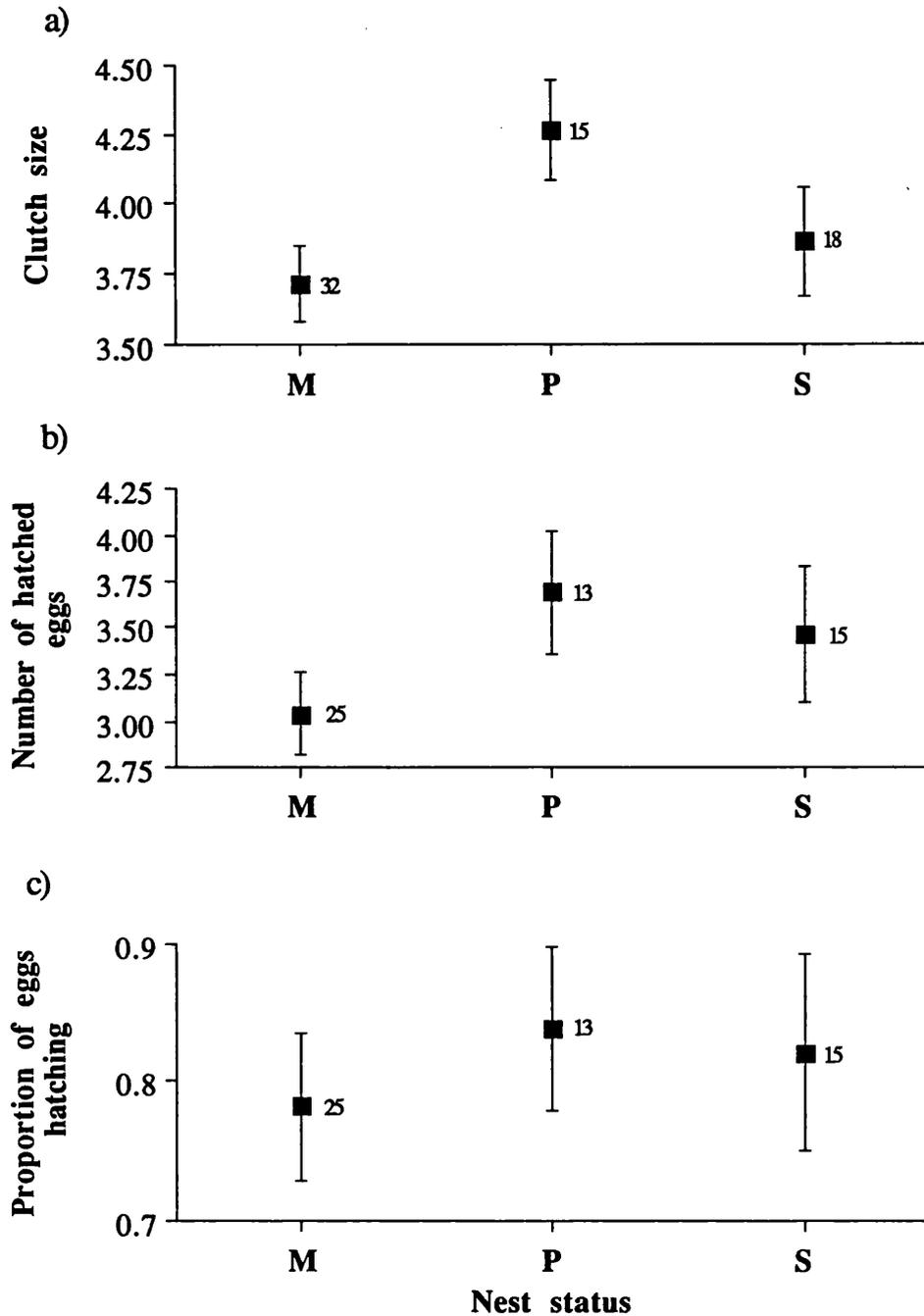


Fig. 3.5. Clutch parameters (mean \pm s.e., n) against nest status (M = monogamous, P = primary and S = secondary), for a) clutch size b) number of hatched eggs and c) proportion of hatched eggs. There were no significant differences between nests of each status for any parameter (Kruskal Wallis ANOVA; a) $H = 5.00$, $df = 2$, $p < 0.1$; b) $H = 2.85$, $df = 2$, $p > 0.1$; c) $H = 0.362$, $df = 2$, $p > 0.5$).

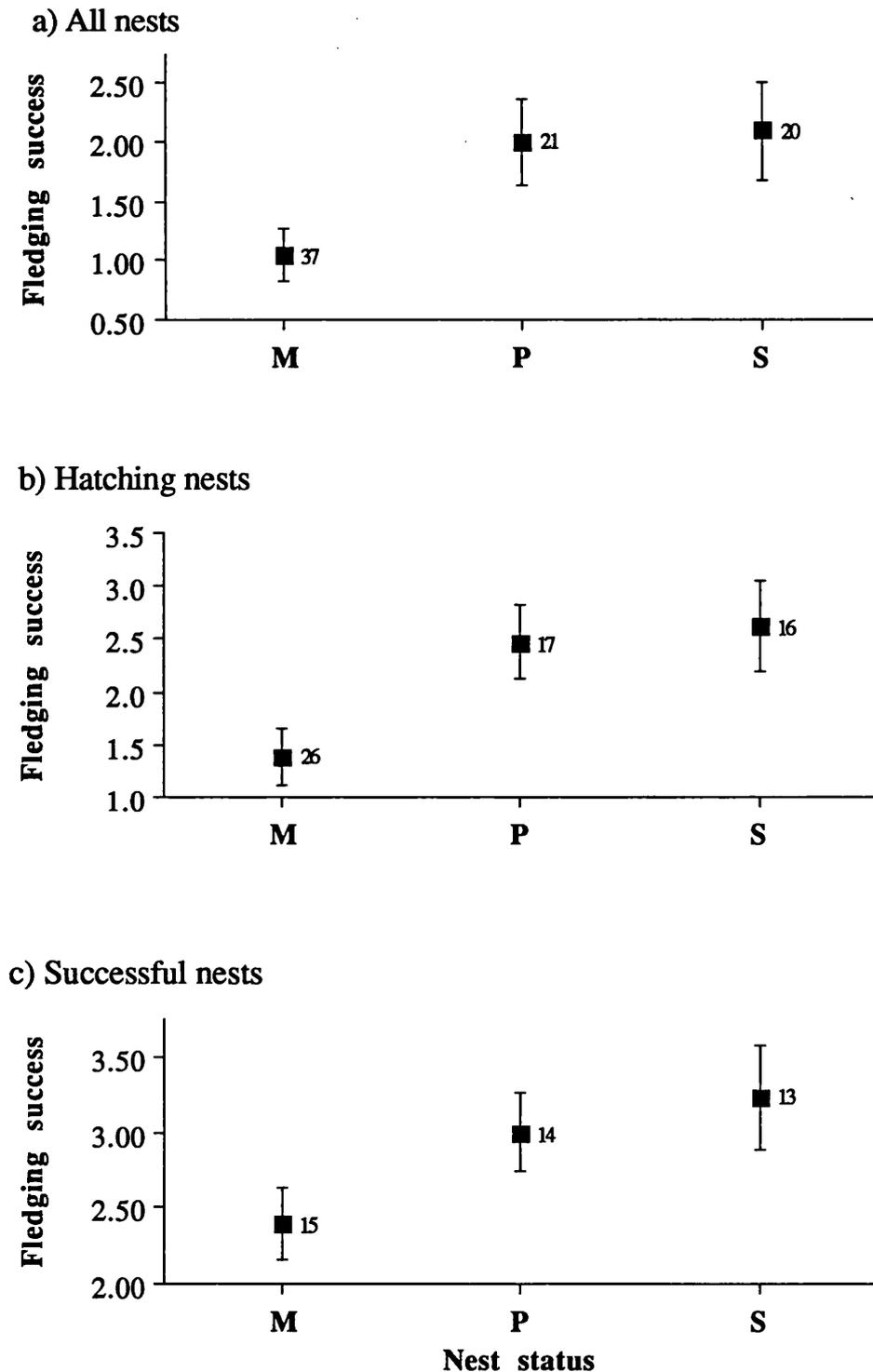


Fig. 3.6. Fledging success (mean \pm s.e., n) against nest status (M = monogamous, P = primary and S = secondary), for a) all nests, b) nests which hatched at least one egg and c) nests which fledged at least one chick. In a) and b) nests of monogamous females had a significantly lower fledging success than nests of primary and secondary females, but in c) there was no significant difference between the groups (Kruskal-Wallis ANOVA; a) $H = 6.88$, $df = 2$, $p < 0.05$; b) $H = 7.87$, $df = 2$, $p < 0.025$; c) $H = 4.36$, $df = 2$, $p < 0.1$; Pair-wise comparisons, Mann-Whitney; a) M vs P, $z = 2.22$, $p < 0.03$; M vs S, $z = 2.15$, $p < 0.04$; P vs S, $z = 0.19$, $p < 0.9$; b) M vs P, $z = 2.34$, $p < 0.02$; M vs S, $z = 2.33$, $p < 0.02$; P vs S, $z = 0.33$, $p < 0.8$).

3.4. Discussion

Using DNA fingerprinting, it has shown that there was no intra-specific brood parasitism (IBP) found in this study (Chapter 2). Observations of nest contents also failed to provide any evidence for IBP. If females had been victims of IBP by other females this should have been apparent through the apparent laying of more than one egg per 24-hour period; this was not observed for any nest. Alternatively, the parasitic female could have removed one of the host's eggs before laying her own, but no single eggs were recorded as disappearing (other than to predation by small rodents) and as they were all numbered this would have been noticed. Eggs were also physiognomically variable between females and any 'foreign', dumped eggs would have stood out from the rest of the clutch. In this case, therefore, female reproductive success can be accurately measured by observation of the nest contents.

3.4.1. Timing of breeding

On North Uist the peak egg laying period for first clutches in 1989-90 was the first fortnight of June, although some first clutches were even laid as late as early August. It is unlikely that these females had attempted to breed outside the study site and then moved into it, as observations of colour-ringed birds showed that females never moved from one breeding area (such as Balranald) to another, either within or between years (M. Shepherd and I.R. Hartley in prep.). Relays are obviously later, peaking around early July, and second broods are the last clutches to be laid, usually around early to mid-August.

Other studies have shown variable breeding periods. Hegelbach (1984) studied a colour ringed population in Switzerland for 10 years and found that most clutches were laid between mid-May and mid-July, with the earliest being 5th May and the latest being 20th July. This was approximately 3 weeks earlier than in the present study. In Cornwall, England, Ryves and Ryves (1934a, b) found that most clutches were completed between early June and early August and MacDonald (1965) found a similar breeding period in Sutherland, Scotland. Walpole-Bond (1931, 1938) found nests between the end of May and the end of August in Sussex, England.

From these few studies it seems that the Swiss population studied by Hegelbach (1984) bred earlier in the year than the British population(s). The main behavioural difference between the two populations is that Swiss corn buntings are migratory, wintering away from the breeding site, whereas in Britain most populations are apparently sedentary. The majority of British-ringed corn bunting recoveries are within 9 km of the ringing site (Mead and Clark 1987). Corn buntings on North Uist are sedentary and no birds breeding on Balranald were seen elsewhere on the Uists or Balranald. Three birds ringed in the Balranald area in winter were found breeding elsewhere on the Uists, one at Borve on Benbecula, one at Newton at the north end of North Uist and one on Baleshare on North

Uist. None of these movements was over 35 km and they probably represent local winter movements rather than migrations. Continental birds may breed earlier in order to allow themselves more time to recover body condition for autumn migration.

3.4.2. First egg dates, clutch size and breeding success

Clutch sizes reported in this study are similar to those reported from elsewhere in Britain, although Gliemann (1972) found significantly larger clutch sizes for his German population (Mann-Whitney, $z = 3.877$, $n = 17$ and 56 , $p < 0.0001$). There is a general tendency for clutch sizes of the same species to be slightly smaller in Britain than the rest of Europe and this may be due to differences in food supply caused by the cooler, wetter climate of Britain (Lack 1954). Table 3.3 shows the clutch sizes from different studies. Other studies did not differentiate between first clutches and relays.

Breeding success was apparently highly variable between studies; but most authors did not find all the nests on their study sites and so their measures of success are of limited use because nests with young would be the easiest to find and these would bias the data. Table 3.3 shows the fledging success data produced by different studies.

Neither the present study nor Hegelbach (1984) found any significant relationship between FED and first clutch size, and there was no relationship between FED and fledging success of successful nests or between FED and proportion of the clutch hatching. For first clutches, early nests tended to fail more often than late ones because of both nest predation and chick starvation. It is difficult to separate these two types of nest failure as hungry chicks usually call more which may attract predators. These results indicate that corn buntings may not be under extreme pressure to lay and rear a brood as quickly as possible, as has been suggested for the migratory pied flycatcher (Alatalo *et al.* 1981, 1982; Slagsvold *et al.* 1988). Alatalo *et al.* (1981, 1982) suggested that the short breeding season of the pied flycatcher, combined with a decrease in breeding success later in the season, restrained females from assessing the true status of mated, polyterritorial males. They suggested that the combination of male polyterritoriality and the female's shortage of time prevented females from assessing the true mated status of males and this led to polygyny in this species (but see Järvi *et al.* 1982; Meier 1983; Stenmark *et al.* 1988; and reply by Alatalo *et al.* 1984a). It is likely that female corn buntings can assess the true status of males, as they are only rarely polyterritorial (M. Shepherd and I.R. Hartley unpublished data) and polygynous females were often seen together on male territories. Female pied flycatchers nesting later in the season obtained lower quality nest holes which were more susceptible to predation (Alatalo *et al.* 1988; Slagsvold *et al.* 1988). As corn buntings are ground nesting passerines they may not be limited by nest site quality to the same extent as hole-nesting pied flycatchers. The apparently reduced urgency for females to nest as early as possible means that they may be free to wait for a mated male's first female to finish

Study area	Clutch size		Mean fledging success (n)					reference
	mean (n)	S.D.	range	all nests	hatched nests	fledged nests		
Sussex, U.K.	'4 - 5' (-)		3 - 6	-	-	-	1,2	
Cornwall, U.K.	4.05 (38)	0.868	2 - 5(6)	2.72 (53)	-	3.6 (40)	3,4	
Sutherland, U.K.	3.94 (17)	0.66	3 - 5	-	2.68 (14)	2.80 (15)	5	
Germany	4.71 (17)	0.686	3 - 6	3.08 (37)	3.68 (31)	4.22 (27)	6	
Switzerland	4.12 (25)	1.05	2 - 6	-	-	3.2 (113)	7	
N. Uist, U.K. (1st)	3.75 (36)	0.649	2 - 5	1.36 (47)	1.74 (38)	2.75 (24)	present study	
N. Uist, U.K. (relay)	4.00 (20)	0.858	2 - 5	1.92 (25)	2.67 (9)	3.00 (16)	present study	

References: 1. Walpole - Bond 1931; 2. Walpole - Bond 1938; 3. Ryves and Ryves 1934a; 4. Ryves and Ryves 1934b; 5. MacDonald 1965; 6. Gliemann 1972; 7. Hegelbach 1984.

Table 3.3. Clutch size and fledging success data from five published studies and the present study.

breeding before laying on the same territory, thus reducing (or possibly as a result of) female-female competition (see chapter 6).

Corn buntings do not have smaller clutches later in the season as found in some other species (e.g., Perrins 1965; Newton and Marquiss 1984; Alatalo *et al.* 1981), which is a further indication that there is a lower urgency to breed, in relative terms, although females may benefit from nesting early by leaving themselves more time to renest if the first nest fails.

3.4.3. Relays and second broods

Relays were common in the study population, with 86.4% of failed females trying again. Female corn buntings did not lay smaller relay clutches than first clutches. If females were depleted of stored muscle or fat reserves they might have expected to have laid smaller clutches due to a decrease in body condition. Unfortunately, data were not obtained on individual females' weight changes and so it was not possible to test whether female body condition changed between clutches.

Second broods were rare and this was also found to be the case in Switzerland (Hegelbach 1984). This was probably due to a time constraint because the breeding season is only just long enough for two successful nesting attempts. This was supported by the data presented here because those successful first broods which were followed by second broods were significantly earlier than those which were not.

3.4.4. Effects of female age on reproductive success

Other studies have found that older females have a higher reproductive success than younger females (e.g., Perrins 1965; Coulson 1966; Mills 1973; Newton *et al.* 1981; Harvey *et al.* 1985; Perrins and McCleery 1985; Shaw 1985; Gustafsson and Pärt 1990; Pärt 1991). The results from this study do not show any relationship between female age and either fledging success or nest status. These results are, however, based on small sample sizes and the data here are not sufficiently conclusive for investigating the effects of age on reproductive success in this species.

3.4.5. Female reproductive success in relation to the mating system

It is clear from the data presented here that female corn buntings which mated polygynously did not suffer reduced reproductive success as a result. In fact, in contrast to many other polygynous passerine species, polygynously mated female corn buntings were more successful than monogamous females.

Timing of breeding affects reproductive success in some species (e.g., Perrins 1965; Lack 1966; Alatalo and Lundberg 1984; Newton and Marquiss 1984), either because lower quality territories are occupied later, lower quality females settle later or there is a

reduction in environmental resources (such as food) as the breeding season progresses.

In this study, later breeding females did not suffer reduced reproductive success. Nests tended to fail more often early in the season, possibly because nesting cover was less dense then, but for nests which fledged at least one young there was no significant correlation between fledging success and first egg date. This may have partly explained why nests of secondary females were equally as successful as those of primary females, but not why monogamous females were less successful. Nests of monogamous females were no earlier or later than nests of primary females, so timing of breeding could not have been the reason for the difference in success.

The fact that fledging success did not decline with breeding date could be because male territories were all of similar quality for the resource crucial to female reproductive success, such that later settling females were not disadvantaged in being only able to choose from a lower quality set of territories.

It has been suggested that nuptial feeding can be a valuable source of food for females preparing to lay, as it may increase the clutch size or advance the laying date (Lifjeld and Slagsvold 1986; Lifjeld *et al.* 1987), but it did not occur in this study. The reduced breeding success of monogamous females was not due to smaller clutch sizes or differential hatching success, so although all three nest classes started out with similar nest contents, monogamous females fledged fewer young than bigamous females. It was not likely that this was due to greater predation at monogamous nests because completely failing monogamous nests were no more likely to be either predated or deserted/starved than completely failing nests of bigamously mated females. In any case, there was no evidence to suggest that polygynous females gained from each other in terms of nest defence; I was never mobbed by more than one female at a nest while ringing the chicks, even on the territories of bigamous males. This contrasts with a study on red-winged blackbirds, which showed that polygynously mated females gained benefits from each other in terms of better nest defence (Picman *et al.* 1988).

Monogamous nests seemed to suffer greater partial chick mortality than bigamous nests, although this was not statistically significant. Differences in mortality may result from variation among nest classes in the amount of food provided to each chick. A reduced provisioning rate is usually what is expected for secondary nests of polygynous males rather than monogamous nests, but this assumes that the food delivered by the male is important, which it has been shown to be in 11 out of 16 passerine species (Davies 1991). It may be that, in corn buntings, male feeding effort is relatively unimportant in the diet of the nestlings compared to that of females, or that monogamous males do not help at all because they are trying to attract a second mate. The latter seems unlikely when considering the evidence from observations and experiments on male song which suggests that females do not use cues from the male when deciding where to breed (M. Shepherd

pers. comm.). Chapter 4 investigates the roles of males and females in provisioning the nestlings.

3.5. Summary

1) Reproductive success of female corn buntings is described in relation to the mating system.

2) On the study site the first clutches were started in early June and clutches were laid until the end of August. Second broods were rare but most females which failed during the first nesting attempt later relayed.

3) Clutch size per nest averaged 3.75 for first clutches and 4.00 for relays, and fledging success per nest averaged 2.75 for first clutches and 3.00 for relays. Relays and first clutches were statistically indistinguishable for all clutch size and success parameters.

4) Fledging success increased with later time of breeding, unlike in some other species. This may have been because, a) male territories were similar for the resource required by nesting females, b) poorer quality females did not settle later than other females or c) environmental factors did not reduce significantly with the progression of the season.

5) Unlike most other polygynous birds, primary and secondary females of polygynous male corn buntings had similar reproductive success and both had greater reproductive success than monogamous females.

6) Monogamous females had lower reproductive success because their chicks starved more, possibly because they were provisioned differently to nests of polygynously paired females.

Chapter 4. Provisioning of nestlings by each sex in relation to the mating system

4.1. Introduction

4.2. Methods

4.3. Results

4.3.1. Food provisioning rates and brood size

4.3.2. Food provisioning rates and nestling age

4.3.3. Food provisioning rates and nest status

4.3.4. Load sizes and nest status

4.3.5. Temporally overlapping nests on the same territory

4.4. Discussion

4.4.1. Variation in brood value: certainty of paternity

4.4.2. Variation in brood value: brood size and nestling age

4.4.3. Sexual differences in costs of provisioning

4.5. Summary

4.1. Introduction

Reproductive effort consists of mating effort (ME), such as males singing to attract females or female choice of a male, and parental investment (PI) which is put directly into raising offspring, e.g., nest building, incubating and nestling provisioning (Trivers 1972; Low 1978; Silver *et al.* 1985; Clutton-Brock 1991), although some behaviours could constitute both ME and PI (Clutton-Brock 1991). Males of polygynous species generally provide much less PI than those of monogamous species (Lack 1968; Silver *et al.* 1985; Clutton-Brock 1991), possibly because males of polygynous species achieve greatest fitness by increasing the ME:PI ratio of their reproductive effort (Emlen and Oring 1977). If more pairing/mating opportunities are available, males should put more effort into trying to obtain further mates, or extra-pair copulations (EPCs), and investment in rearing offspring may be correspondingly less.

In some polygynous bird species, male parental care, in terms of provisioning of nestlings, has no significant effect on female reproductive success. In one population of yellow-headed blackbirds, for example, males provided few feeds to each nest and female reproductive success was not affected by the male contribution (Crawford 1977; Lightbody and Weatherhead 1987, 1988; but see Willson 1966 and Patterson *et al.* 1980). In other polygynous species, however, male provisioning investment has a significant effect on female reproductive success. In pied flycatchers, secondary females of polygynous males have a lower reproductive success than primary females of the same males because the majority of male nestling provisioning investment is directed towards the

primary nests (Alatalo *et al.* 1981, 1982; Lifjeld and Slagsvold 1990). Polygynous, male great reed warblers show a similar skew of paternal provisioning investment towards their primary nests (Catchpole *et al.* 1985; Drycz 1986; Urano 1990), although in warmer climates secondary females do as well as primary females because they are emancipated from the costs of brooding young and so can compensate for the feeds that the male does not provide (in Urano 1990).

Male parental care in the polygynous red-winged blackbird is highly variable both between and within populations (Searcy and Yasukawa 1989). In some populations, males feed the young of the primary female almost exclusively (Patterson *et al.* 1980; Yasukawa and Searcy 1982), whereas in other populations males divide parental care evenly between females (Muldal *et al.* 1986). It is clear, however, that male provisioning of nestlings enhances female reproductive success (Muldal *et al.* 1986; Patterson *et al.* 1980; Yasukawa and Searcy 1982).

In other polygynous passerines, males direct most parental care towards nests of their primary females, e.g., bobolinks (Martin 1974; Wittenberger 1978, 1980a, 1982; but see also Wootton *et al.* 1986), marsh wrens (Leonard and Picman 1987; Leonard 1990), song sparrows (Arcese 1989), house sparrows (Veiga 1990), Japanese wagtail (in Webster 1991) and some populations of yellow-headed blackbirds (Crawford 1977; Patterson *et al.* 1980). In other species, males evenly divide their provisioning investment between their females e.g., dunnocks (Davies 1986) and some populations of bobolinks (Wootton *et al.* 1986), or rarely feed any nest at all e.g., dickcissels (Zimmerman 1966) and some populations of indigo buntings (Carey and Nolan 1979).

Male parental care may be asymmetrically allocated to nests either because broods are valued differently by each sex (Ridley 1978; Winkler 1987; Møller 1988, 1991b; Westneat 1988; Burke *et al.* 1989; Lifjeld and Slagsvold 1991; Weatherhead and McRae 1990) or males and females may incur different costs to parental investment (Searcy 1979a; Houston and Davies 1985; Hughes and Hughes 1986; Smith *et al.* 1988).

Parental care includes many aspects of parental investment such as nest building, egg incubation, offspring defence, nestling provisioning and others, but provisioning is thought likely to be the most costly aspect of parental care in birds (Drent and Daan 1980; Clutton-Brock 1991). This chapter looks at provisioning of nestlings in relation to the polygynous mating system of the corn bunting. In particular, the relative amounts of nestling provisioning done by each parent are evaluated for nests of monogamous, primary and secondary females, and provisioning is discussed with respect to brood value and the overall contribution of male parental investment to female reproductive success. Previous studies found that male corn buntings rarely, if ever, provided nestling feeds (Walpole-Bond 1931; Ryves and Ryves 1934a, b; MacDonald 1965; Gliemann 1973; Møller 1983) and took no other part in parental care. In a study of colour-ringed corn buntings,

however, Hegelbach (1984) found that males did provide some nestling feeds but much less than the females, and males played no other role in parental care.

4.2. Methods

After hatching, chicks were in the nest for 9 - 12 days after which time they were fed for up to three weeks. All the observations in this study refer to young which were in the nest, as opposed to fledglings. Individual nests were observed for one-hour periods during morning (05:00 - 08:00 h), afternoon (12:00 - 15:00 h) and evening (18:00 - 21:00 h) time periods, when nestlings were 0 - 3, 4 - 7 and 8+ days old. Fifty-three nests (25 in 1989, 28 in 1990) were used to give a total of 320 hours of observations (mean \pm s.d. = 6.23 ± 2.50 hours per nest). Observations were carried out from a car at distances of 10 - 40 m from the nest using binoculars or a telescope. At each nest visit the following were recorded:- time of entry to nest, sex of provisioning adult, food load size, destination habitat (chapter 5) and distance travelled to first foraging site (chapter 5). Food load size was estimated by comparison to the bill and sizes were categorized as large, medium or small. A small load generally consisted of one or two small items held in the tip of the bill, medium loads were one large item or a number of small items visibly held in more than just the tip of the bill and large loads were two or more large items (e.g., large caterpillars) hanging from the bill or a number of smaller items completely filling the bill so that most of it was not visible because of protruding food.

Corn buntings are sexually monochromatic for plumage, so the sex of provisioning parents was identified from either colour ring combinations or from white, typists' correction fluid (Tippex) markings which were painted onto one or two secondary coverts of the females' wings.

Nest status was assigned as described in chapter 1 and trigamous nests were not included in the analyses due the small sample size ($n = 3$).

4.3. Results

Male corn buntings took no part in nest building, egg incubation or chick brooding, but contrary to other studies (Walpole-Bond 1931; Ryves and Ryves 1934a, b; MacDonald 1965; Gliemann 1973; Møller 1983) males were seen to provision nestlings at most nests.

4.3.1. Food provisioning rates and brood size

Male feed rate (feeds per hour) increased with brood size in the 4 - 7 day old age group, although not significantly (for statistical tests see Fig. 4.1a). There was no clear pattern to male food provisioning rates in relation to brood size for age groups 0 - 3 and 8+ days (Fig. 4.1a). Females tended to increase their feed rate with increasing brood size in all age classes, although this was significant only in the 0 - 3 day age class (for statistical tests see

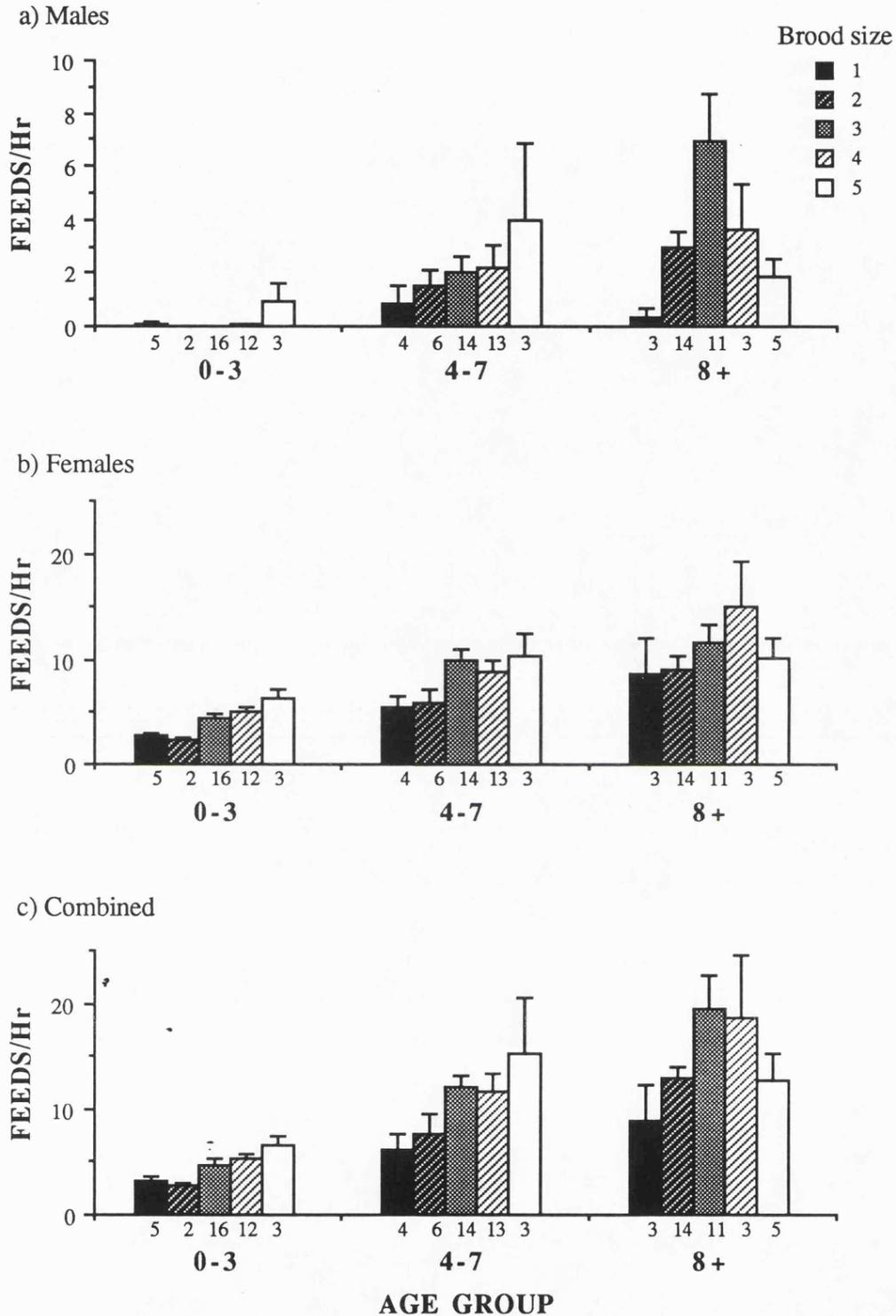


Fig. 4.1. Feed rates (feeds per hour) for broods of different sizes within age groups (brood age in days) for a) males, b) females and c) males and females combined (bars show mean + s.e., sample sizes are shown under bars). Feed rate generally increased with brood size for females and combined parents feeding broods at 0 - 3 days old, but not for age groups 4 - 7, 8+ or any male chick age group (Kruskal-Wallis tests, all $df = 4$: a) males, 0 - 3, $H = 3.51$, $p < 0.5$; 4 - 7, $H = 1.60$, $p < 0.7$; 8+, $H = 7.83$, $p < 0.1$ b) females, 0 - 3, $H = 13.1$, $p < 0.02$; 4 - 7, $H = 8.24$, $p < 0.1$; 8+, $H = 4.68$, $p < 0.5$ c) combined, 0 - 3, $H = 10.6$, $p < 0.05$; 4 - 7, $H = 9.07$, $p < 0.1$; 8+, $H = 5.13$, $p < 0.3$).

Fig. 4.1).

The combined male and female feed rate also tended to increase with increasing brood size, although again this was significant only in the 0 - 3 day age class (for statistical tests see Fig. 4.1c), essentially reflecting the component female-only result, as males fed very little at this age.

The trend for increasing feed rate with increasing brood size is probably a real one, at least in females, and the lack of statistical significance in the results is likely to be a reflection of the small sample sizes. The food provisioning rates in sections 4.3.2 and 4.3.3 are expressed as feeds per chick per hour to control for brood size.

4.3.2. Food provisioning rates and nestling age

Not all males fed their nestlings but the proportion which did feed increased with nestling age ($\chi^2 = 36.3$, $df = 2$, $p < 0.001$; Fig. 4.2). Two of the males which were not seen to feed in the 8+ day category were seen feeding in the 4 - 7 day age group but otherwise males seen feeding one age group were always seen to feed at the later stages too.

All females provisioned their nestlings, although one female disappeared (presumed predated) during the nestling period and the male successfully fledged the brood, of three, on his own. Provisioning by extra-pair males occurred at two nests but consisted of only one or two small feeds each as they spent more time following the pair female. One of these males was recorded on only a single one-hour watch then was not seen subsequently; the other took up a new territory quite late in the season in which a female paired to an adjacent male had already built a nest and laid eggs before he arrived.

Both male and female feed rate (feeds per chick per hour) increased significantly with chick age (see Fig. 4.3a for statistical tests). In both sexes the increase was greatest between age groups 0 - 3 and 4 - 7, with a smaller increase between 4 - 7 and 8+ days.

Males provisioned at a lower rate than females overall (Wilcoxon signed rank test, $z = 9.13$, $p < 0.0001$) and also within each age class (Wilcoxon signed rank tests; 0 - 3, $z = 5.71$, $p < 0.0001$; 4 - 7, $z = 5.57$, $p < 0.0001$; 8+, $z = 4.69$, $p < 0.0001$). On average, males provided only 2.9% of feeds during age group 0 - 3 days, 17.7% at 4 - 7 days and 22.0% at 8+ days (Fig. 4.3b). The increase in the proportion of male:total feed rate with increasing chick age was significant (for statistical tests see Fig. 4.3b).

4.3.3. Food provisioning rates and nest status

There were no significant differences between nests of monogamous, primary and secondary females for either male, female or total food provisioning rates (feeds per chick per hour) in any age group (for statistical tests see Fig. 4.4).



Fig. 4.2. Proportion of nests in each nestling age group which received, and did not receive, male feeds. Sample size is shown under each pair of bars. The proportion of nests which received male feeds increased significantly with nestling age ($\chi^2 = 36.3$, $df = 2$, $p < 0.001$).

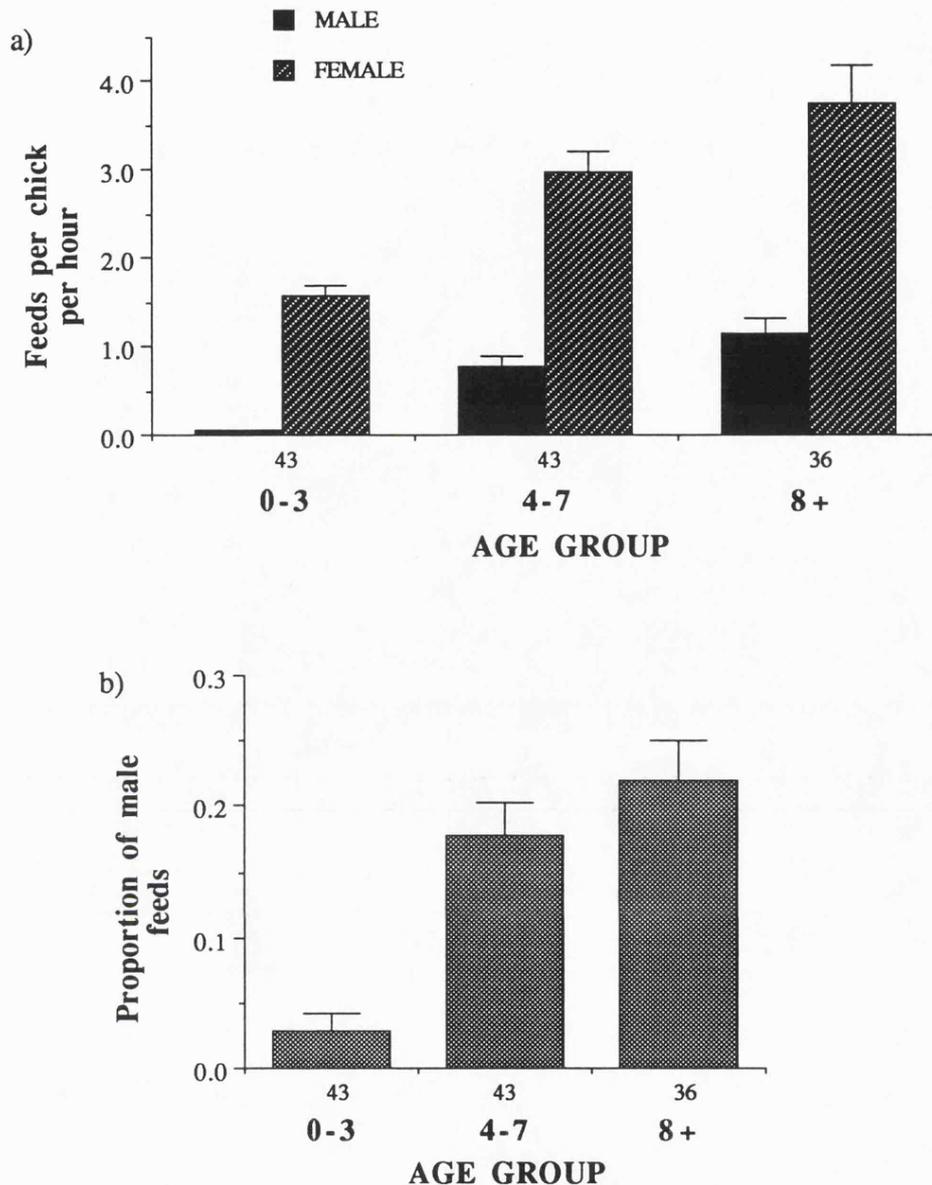


Fig. 4.3. Feed rates (feeds per chick per hour) for broods of different ages (mean + se, n) for a) males and females and b) proportion of male feeds divided by total feeds. Both males and females fed older broods significantly more than younger broods (Kruskal-Wallis ANOVAs: a) males, $H = 41.9$, $df = 2$, $p < 0.001$; females, $H = 38.2$, $df = 2$, $p < 0.001$) and females had a significantly higher feed rate than males in all age classes (Wilcoxon signed rank tests; 0-3, $z = 5.71$; 4-7, $z = 5.57$; 8+, $z = 4.69$; in all three cases $p < 0.0001$). The proportion of male feeds (b) increased significantly as broods became older (Kruskal-Wallis ANOVA, $H = 35.7$, $df = 2$, $p < 0.001$). In both cases there were significant pair-wise comparisons between the 0-3 vs 4-7 and 0-3 vs 8+ age groups, but not between 4-7 vs 8+ age groups (Mann-Whitney tests; a) Males: 0-3 vs 4-7, $z = 4.76$, $p < 0.0001$; 0-3 vs 8+, $z = 6.42$, $p < 0.0001$; 4-7 vs 8+, $z = 1.71$, $p < 0.09$; Females: 0-3 vs 4-7, $z = 4.94$, $p < 0.0001$; 0-3 vs 8+, $z = 5.56$, $p < 0.0001$; 4-7 vs 8+, $z = 1.14$, $p < 0.0001$ b) Proportion of male feeds: 0-3 vs 4-7, $z = 4.59$, $p < 0.0001$; 0-3 vs 8+, $z = 5.91$, $p < 0.0001$; 4-7 vs 8+, $z = 1.01$, $p < 0.27$).

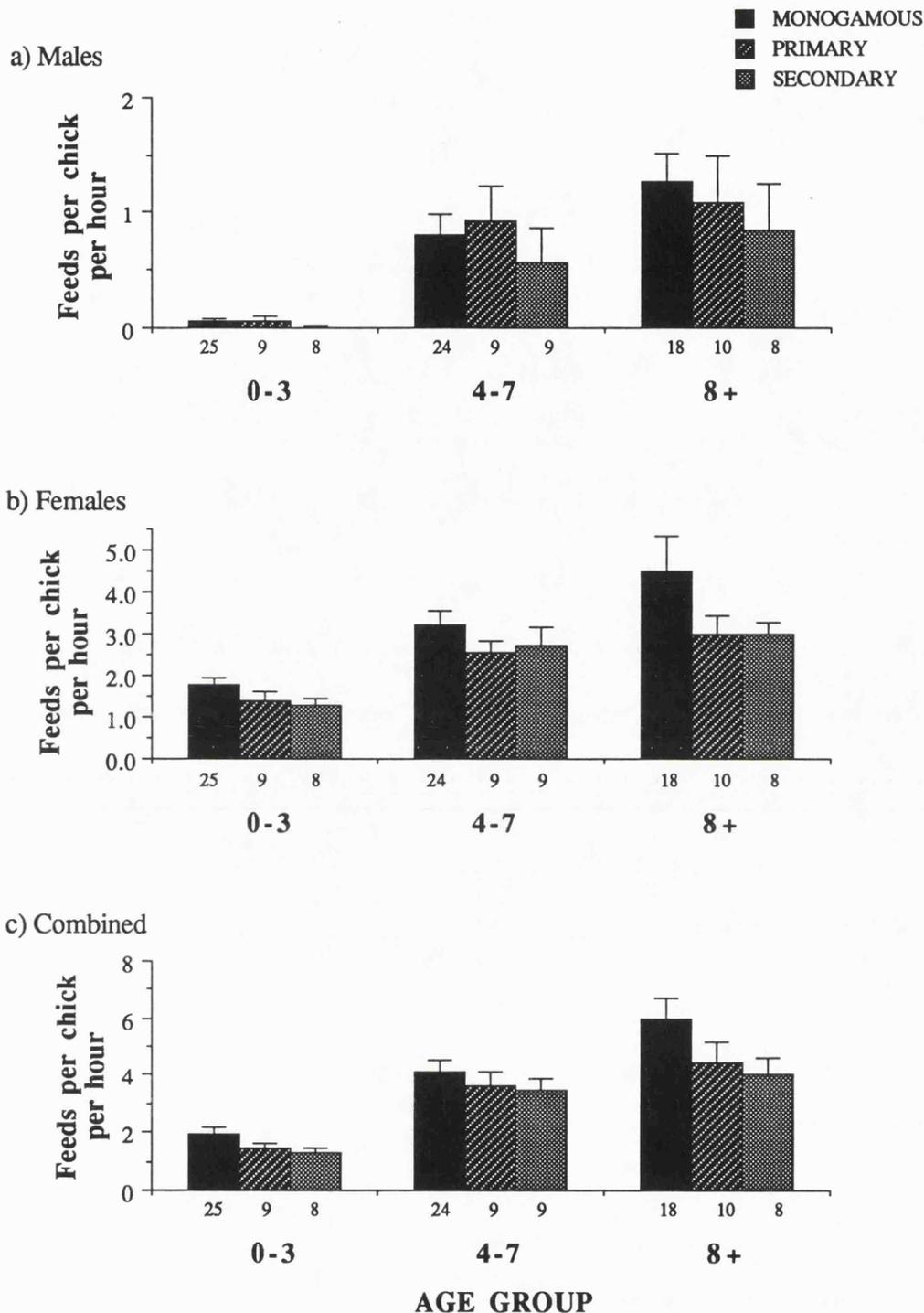


Fig. 4.4. Feed rates (feeds per chick per hour) for nests of monogamous, primary and secondary females in each age group (age in days) for a) males, b) females and c) males and females combined (bars show mean + s.e., n). There were no significant differences in feed rate between monogamous, primary and secondary nests within any age class for male, female or combined feed rates (Kruskal-Wallis ANOVAs, all $df = 2$; a) males 0-3, $H = 0.44$, $p < 0.9$; 4-7, $H = 1.59$, $p < 0.5$; 8+, $H = 1.67$, $p < 0.5$; b) females 0-3, $H = 1.59$, $p < 0.5$; 4-7, $H = 0.73$, $p < 0.7$; 8+, $H = 1.73$, $p < 0.5$; c) combined 0-3, $H = 2.11$, $p < 0.3$; 4-7, $H = 0.80$, $p < 0.7$; 8+, $H = 3.98$, $p < 0.1$).

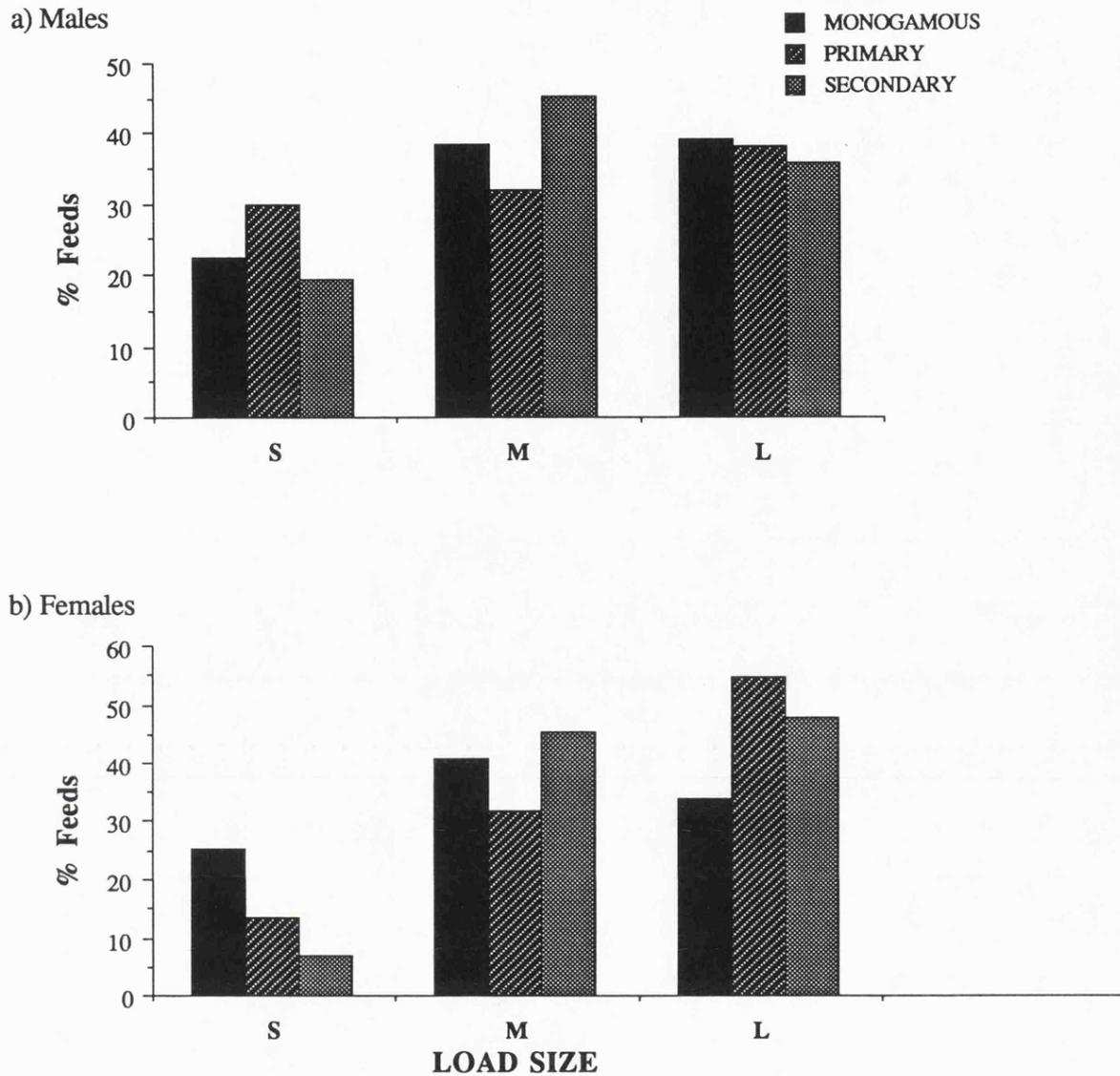


Fig. 4.5. Proportions of food deliveries in different size classes (L = large, M = medium, S = small) for a) males and b) females, at monogamous, primary and secondary nests. Males did not show any significant differences between nest classes for load size ($\chi^2 = 5.24$, $df = 4$, $p < 0.3$). Females showed significant differences between nest classes for load size, with monogamous nests receiving more small loads and fewer medium and large loads than expected, whereas primary and secondary females did not differ in load sizes ($\chi^2 = 75.1$, $df = 4$, $p < 0.0001$).

4.3.4. Load sizes and nest status

The total frequencies of large, medium and small food loads delivered by males were not significantly different between nests of monogamous, primary and secondary females ($\chi^2 = 5.24$, $df = 4$, $p < 0.3$; Fig. 4.5a). Total delivery frequencies of large, medium and small food loads by females were significantly different between nest classes, with nests of monogamous females receiving more small loads and fewer large loads than expected, whereas both primary and secondary females' nests received more large loads than expected ($\chi^2 = 75.1$, $df = 4$, $p < 0.0001$).

Frequencies of male and female load sizes were similar within nests of monogamous females ($\chi^2 = 1.94$, $df = 2$, $p < 0.4$), although in nests of primary and secondary females, females delivered more large loads and fewer small loads than males (primary, $\chi^2 = 16.5$, $df = 2$, $p < 0.0005$; secondary, $\chi^2 = 14.0$, $df = 2$, $p < 0.001$).

4.3.5. Temporally overlapping nests on the same territory

Two bigamous males had primary and secondary females which overlapped their nestling periods by more than one day. The first male had six days overlap of the nestling period and fed only the secondary female's brood. The second male had an overlap of seven days and fed both nests approximately equally (when taking chick age into account) during the overlapping period. It seems, therefore, that males are able to feed two nests at the same time, although data were sparse for overlapping nests.

4.4. Discussion

Polygynous males did not distribute their nestling provisioning investment asymmetrically between the nests of their primary and secondary females, as many other polygynous birds do (Martin 1974; Crawford 1977; Patterson *et al.* 1980; Wittenberger 1978, 1980a, 1982; Alatalo *et al.* 1981, 1982; Catchpole *et al.* 1985; Drycz 1986; Leonard and Picman 1987; Arcese 1989; Leonard 1990; Lifjeld and Slagsvold 1990; Urano 1990; Veiga 1990; Webster 1991). Males provisioned nests of monogamous, primary and secondary nests at similar rates and with similar sized food loads. Males provided less nestling feeds than females, rarely provided food before chicks were four days old and, even at the later stages of the nestling period, provided a mean of only 22% of the total feeds.

Nests of monogamous, primary and secondary females received similar female food provisioning rates but monogamous females delivered more small food loads than primary or secondary females, possibly leading to the reduced reproductive success of monogamous females (chapter 3).

Possible reasons for polygynous males symmetrically apportioning feeds between nests

are:-

1) Broods may be of similar value to the male, either genetically (Hamilton 1964; Ridley 1978; Winkler 1987; Møller 1988; Westneat 1988; Burke *et al.* 1989; Weatherhead and McRae 1990) or because of brood size or age (Lifjeld and Slagsvold 1991).

2) Males and females may incur different costs of parental care (Searcy 1979a; Houston and Davies 1985; Hughes and Hughes 1986; Smith *et al.* 1988).

Each of these reasons are now discussed in more depth.

4.4.1. Variation in brood value: certainty of paternity

Offspring are likely to be more valuable to females than to males because birds have internal fertilization (Trivers 1972; Clutton-Brock 1991), which means that females are more certain of maternity than males are of paternity and so are more likely to be closely related. In this study, extra-pair paternity was rare (chapter 2) so polygynous male corn buntings may have valued primary and secondary broods similarly for paternity assurance and, therefore, provided them with equal amounts of nestling feeds.

Males of polygynous and polyandrous species may be more likely to reduce paternal care, due to uncertainty of paternity, than males of monogamous species. Males of polyandrous dunnocks share the female with a male counterpart which is inversely uncertain of his paternity, and so both males should, and do, feed nestlings in relation to their expected paternity (Houston and Davies 1985; Burke *et al.* 1989; Davies *et al.* in press). Extra-trio paternity is rare within polyandrous groups of dunnocks and so males which feed in proportion to their expected paternity are making a correct decision. In polygynous species, males which are not certain of their paternity could possibly increase their fitness by seeking extra females, rather than feeding young which may have been sired by extra-pair copulations. Males of polygynous species may be more likely to be uncertain of their paternity than monogamous species because they may have to trade off mate-guarding the primary female against guarding subsequent females (Arak 1984; Alatalo *et al.* 1986a; Davies 1991; Hasselquist and Bensch 1991).

Whether or not a male in any mating system should reduce his feeding rate in accordance with certainty of paternity should depend on the benefits to be gained from investing elsewhere, either in other nests or seeking other mating opportunities, and the response of the remaining parents to the reduction in provisioning help. If females can make up the shortfall in male feeds by increasing their own investment, males could safely leave to seek other reproductive opportunities. Alternatively, if a female cannot completely make up for the loss of male provisioning investment, a male should trade off other reproductive opportunities against feeding the young.

Empirical evidence concerning certainty of paternity and male parental investment in polygynous species is limited. In the predominantly monogamous indigo bunting, it has

been suggested that males should reduce parental care if they are uncertain about their paternity (Westneat 1988), although in this species males generally provide much less parental care than females (Carey and Nolan 1979; Westneat 1988). The effect of reduced male care may be small for indigo buntings and so the cost of reducing provisioning investment by males may be relatively small.

In polygynous species, where males usually invest most heavily in the young in the nest of the primary female, rates of extra-pair paternity are variable between species. In one population of red-winged blackbirds, for example, 24% of offspring were fathered by extra-pair males (Gibbs *et al.* 1990) but, unfortunately, details of parental investment were not collected. There is great variation in male feeding behaviour in this species (e.g., Patterson *et al.* 1980; Muldal *et al.* 1986) and the pattern of parental care cannot be extrapolated from other populations, so these results are as yet inconclusive in relating paternity to paternal care. Similarly, in bobolinks there is inter-population variation in male parental care behaviour but generally males feed broods of primary females more than those of secondary females (Martin 1974; Wittenberger 1978, 1980, 1982; but see Wootton *et al.* 1986). Extra-pair paternity in this species has been shown to be more common in the broods of primary females of polygynous males than in the broods of secondary females of the same males (Bollinger and Gavin 1991). This result may be contrary to expectation, but again, the paternity analysis has not been combined with parental care observations in the same population.

Weatherhead and McRae (1990) suggested that males of double-brooded pairs of monogamous American robins should allocate parental care according to certainty of paternity because the second clutches were laid whilst the males were feeding the young from the first clutch and were thus unable to mate-guard as efficiently for the second brood. Evidence supporting this idea was not fully convincing as no data on mate-guarding behaviour or paternity was available (Weatherhead and McRae 1990). Møller (1991b) showed that males of double-brooded pairs of monogamous barn swallows did not feed young at the first and second nests differently, but as the males mate guarded their females with equal intensity for both broods, the evidence was not conclusive in determining whether or not males reduced parental care in response to certainty of paternity between broods of the same pair. In a previous study of swallows, Møller (1988) showed that males which were less certain of paternity, through naturally and experimentally low levels of mate guarding, were likely to reduce paternal care to the offspring.

In general it seems that confidence of paternity may influence male parental care, depending on the available reproductive options, but the evidence is very limited. The evidence from this study does not allow a rejection of the theory that males should reduce their parental care in line with reduced paternity assurance because although extra-pair paternity was rare (chapter 2) and males fed nests of primary and secondary females

equally, other factors such as food supply, environmental factors, brood age and brood size may also have had an influence.

4.4.2. Variation in brood value: brood size and nestling age

In this study, the proportion of male feeds divided by total feeds increased as nestlings became older. This could have been because the energy demands of nestlings increased beyond the individual females' capacities to provide sufficient food or the brood may have been less valuable to the male (relative to the female) in its early stages because replacing the brood would take more effort by the female than by the male (Dawkins and Carlisle 1976).

Lifjeld and Slagsvold (1991) carried out an elegant series of experiments on pied flycatchers to show that male parental care was influenced by brood age and brood size. Polygynous males preferentially fed broods which were experimentally manipulated to make them older or larger, independently of the original status of the female (Lifjeld and Slagsvold 1991). Lifjeld and Slagsvold (1991) suggested five factors which could influence a polygynous male's parental investment in one or other brood: hatching interval, inter-nest distance, weather, relative brood size and presence or absence of the female. For corn buntings, inter-nest distance is not likely to be as relevant as it is to polyterritorial species such as the pied flycatcher; weather is out of the control of females. Hatching intervals of pairs of nests on the same territories could potentially be controlled by females, especially in corn buntings which, unlike pied flycatchers, do not suffer a reduction in reproductive success as the season advances (chapter 3). If a male has two nests which simultaneously contain young, he may feed only one nest, increase his parental investment to feed both, or divide his effort between the two nests. Females on the same territory could avoid competing for male attention if they nested asynchronously (Yasukawa and Searcy 1981; Leonard and Picman 1987; Leonard 1990) because males having two simultaneous nests may divide their parental investment equally between the two nests (e.g., Davies 1986; Lifjeld and Slagsvold 1991). Primary and secondary females of polygynous male corn buntings generally had nests which were asynchronous, but they were not less synchronous than expected by chance (chapter 6), so it seems unlikely that pairs of females on the same territories actively spaced themselves in time as has been observed in marsh wrens (Leonard and Picman 1987; Leonard 1990) and some populations of red-winged blackbirds (Yasukawa and Searcy 1981). Of the two males which did have overlapping nestling stages, one did not feed the primary female's brood, but fed the secondary's, and the other divided his feeds between nests.

Females could potentially influence their clutch size and make their broods more valuable by making them larger (Lifjeld and Slagsvold 1991) but clutch sizes in corn buntings did not differ between females of different pairing status (chapter 3). Females

could potentially have been free to desert the nest at the chick stage and leave the male to rear the brood alone. One male, whose female was probably predated, successfully reared a brood alone, so there was the potential for female desertion. It is not likely that desertion would have been a beneficial strategy for female corn buntings, however, as they would have to re-invest much more than the male if the male also deserted and the brood starved.

It seems likely that broods of primary and secondary females were of equal value to male corn buntings in terms of brood size, and that polygynous males were able to feed both nests because they were asynchronous, although females nesting on the same territories apparently did not actively temporally space nests to accommodate this (chapter 6).

4.4.3. Sexual differences in costs of provisioning

The relative costs to parents of provisioning can be divided between direct costs, in terms of reduced body condition and, therefore, survival, and the cost of losing opportunities to engage in other reproductive activities such as seeking extra-pair copulations, attracting extra females or maintaining a territory.

Nest provisioning is probably one of the most energetically costly aspects of avian parental care (Drent and Daan 1980; Clutton-Brock 1991). It has been shown that nestling provisioning is costly in terms of adult survival. In willow tits, parental post-breeding survival decreased as fledging success increased (Ekman and Askenmo 1986), and in house martins, double-brooded females had a lower annual return rate to their breeding sites than single brooded females (Bryant 1979). Experimental brood enlargement has been shown to increase provisioning rate and decrease subsequent survival in pied flycatchers (Askenmo 1977, 1979), collared flycatchers (Gustafsson and Sutherland 1988), blue tits (Nur 1988) and great tits (Lindén 1990), although no effect on adult survival was found in similar experiments with tree swallows (De Steven 1978) and house wrens (Finke *et al.* 1987).

Female corn buntings take on the majority of nestling provisioning, but without experiments to manipulate brood requirements it is not possible to say how this affects their survival. Females are much smaller than males (male weight: female weight ratio = 1.22; Møller 1983) and this may mean that they have different metabolic rates which makes provisioning relatively more costly as well as absolutely more costly to females. It is clear from this study that females work harder at parental investment than males because females do all the nest building, egg incubation and nestling brooding, as well as the majority of the nestling provisioning. As nestlings needed only relatively small amounts of food before day four after hatching, females could provide all that was necessary and males would have more to gain from investing in mating effort. The female, on the other hand, has everything to gain from feeding her nestlings; the best reproductive strategy open to her is

the one that she is currently undertaking. To start again for the female would mean building a nest, laying a new clutch and incubating it to hatching, but up until that stage the male had put no parental investment into the brood. The male could potentially gain from investments directed away from the nestlings whereas the female could make no better investment than in her current clutch/brood. When the nestlings are older and nearer to fledging they require more food and the male's best option, to maximize his reproductive success, is to feed the nestlings.

It is not clear why monogamous females should deliver less food to their nestlings than females paired to polygynous males. Age and experience may be a factor but there is not sufficient data to test this (chapter 3). Female quality may be the answer. Female competition may force low quality females into poor foraging or nesting areas, where either they forage less efficiently because of the lower quality habitat or they are poorer quality foragers *per se* (see chapters 5 and 6). It is possible that, as these females are in low quality areas, other females are less likely to nest there and so they remain monogamous. Low quality females may pair with males of poor quality, which remain monogamous because they cannot hold enough resources for more than one female. Alternatively, female competition may not drive poorer quality females into poorer areas but they could settle in them by making a bad decision which is not repeated by most other females, and so they remain monogamous.

4.5. Summary

1) Males of polygynous bird species usually provide less parental care than the females and often direct paternal care to the nest of the primary female rather than the nests of subsequent females.

2) In corn buntings, males fed less than females in all chick age groups and, on average, provided only 2.9% of feeds when the nestlings were 0 - 3 days old, 17.7% at 4 - 7 days old and 22.0% at 8+ days old. Males fed nests of monogamous, primary and secondary females with similar sized food loads. Females of all pairing status fed nestlings at similar rates but monogamous females delivered smaller loads than primary and secondary females, possibly accounting for reduced fledging success from monogamous nests.

3) The value of broods belonging to primary and secondary females to their males was apparently similar, as extra-pair paternity was very low in this population and brood sizes were similar between nests of primary and secondary females. Males may have been able to feed both nests because they were temporally separate, although at least one male was able to feed overlapping nests simultaneously.

4) The differences in feeds provided by males and females at early and late stages of the nestling period were probably due to sex differences in other available reproductive

opportunities. Females had no better available option than to provide parental care to the current brood, whereas males could potentially increase their fitness by seeking extra matings, pairing with further females or defending a territory in which females could breed.

5) Monogamous females may have provided less food than the primary and secondary females of polygynous males because they were less able parents, although the reasons for this are unclear.

Chapter 5. Territory and habitat use in relation to polygyny

5.1. Introduction

5.2. Methods

5.2.1. Territory mapping

5.2.2. Nesting habitat

5.2.3. Foraging habitat

5.3. Results

5.3.1. Nesting habitat

5.3.2. Male territory habitat

5.3.3. Foraging habitat

5.4. Discussion

5.4.1. Habitat and polygyny

5.4.2. The national corn bunting decline and habitat change

5.5. Summary

5.1. Introduction

In territorial birds, female reproductive success could be affected by the quality of male territories (Searcy 1979a) or male quality itself (Davies 1986). Females choosing where to breed on the basis of territory quality may be selecting potentially good nesting, foraging or chick-rearing areas by direct choice of the resource (Alatalo *et al.* 1986b; Slagsvold 1986), alternatively, they may choose where to nest on the basis of male characteristics, such as plumage, size, song or fighting ability, which may provide an indication of the quality of male territories (Searcy 1979a; Alatalo *et al.* 1990; Arvidsson and Neergaard 1991). The connection between male and territory quality could arise because either the most competitive males win the best territories, or the best territories provide enough resources for the resident males to forage more efficiently and spend more time singing, displaying or otherwise attracting females (e.g., Radesäter *et al.* 1987; Radesäter and Jacobsson 1988; Strain and Mumme 1988; Arvidsson and Neergaard 1991; Davies 1991).

According to the original polygyny threshold model (PTM), polygyny should occur if the quality of breeding situations are so variable between males that females can achieve a higher fitness by pairing with an already paired male in a high quality situation as opposed to an unpaired male in a low quality situation (Verner and Willson 1966; Orians 1969). Although Verner and Willson's (1966) and Orians' (1969) original models were concerned with variability of territory quality, it has since been realised that the 'breeding situation' may include other components which could potentially increase the fitness of the female, such as male parental investment or good genes (Weatherhead and Robertson 1979; Gowaty 1981; Davies 1989).

This chapter examines the relationship between territory composition and mating system variation in corn buntings. If nest site habitat is an important aspect of female reproductive success, then the territories of unpaired males should differ from the those of paired males in the availability of the preferred nesting habitat. Alternatively, if territories are important as a source of food for nestlings, there should be an association between areas of preferred foraging habitats and chick productivity within the territories.

This chapter tests these two hypotheses and describes:-

- 1) Variation in territory vegetation components between males paired with different numbers of females
- 2) Territory use, by each sex, for foraging to provision the nestlings
- 3) Habitat use by the females for nesting.

The study site was especially amenable to tackling this type of problem because farmers on North Uist use a crop rotation system of farming. Cereal crops are rotated in large areas between years, providing a gross experimental manipulation of available habitat. If males are site faithful, but their territory habitat composition changes between years, one could distinguish male quality from territory quality arguments and identify factors guiding female choice of breeding site (e.g., Alatalo *et al.* 1986b; Arvidsson and Neergaard 1991).

Corn buntings have declined over much of Britain in recent years and much of the decline has been attributed to changes in agricultural practices and consequent changes in habitat (Sharrock 1976; Thompson and Gribbin 1986; O'Connor and Shrubbs 1986), although the actual reasons for the decline are unclear. Specifically, there are no available data to suggest that the decline is due to loss of nesting habitat, foraging habitat or other factors, such as changes in winter food availability. This chapter should help to focus future research into the decline of the corn bunting.

5.2. Methods

5.2.1. Territory mapping

Vegetation was mapped over the whole study site in 1989 and 1990 on 1:25 000 Ordnance Survey maps photocopied to the scale of 1:14 300. Habitats were assigned to one of the following categories:

- 1) Cereal (rye and oat mix)
- 2) Fallow (often grazed by cattle)
3. Uncultivated land (e.g., coastal dunes, field margins, hollows and blow-outs)
- 4) Marsh
- 5) Pasture (grazed, but not ploughed for cereal growth within the last 5 years)
- 6) Other (tracks, potato plots, cemetery and hay fields; each < 0.25 hectares).

Male territory boundaries were mapped in each year by looking at interactions between territory holders and day-to-day movements of males. Component habitat categories within

and outside male territories were measured, in hectares, using a plane digitizer (use supplied by Nature Conservancy Council for Scotland).

5.2.2. Nesting habitat

Nest site selection by females was recorded using similar habitat divisions, although for 1989 more detailed habitat was recorded within a 0.5 m.square quadrat (with the nest in the centre). Cover of vegetation family was recorded on a 0-5 dominance scale of cover, where 0 = absent, 1 = <5%, 2 = 5-10%, 3 = 10-25%, 4 = 25-50% and 5 = 50-100%. Such data were available for 35 nests. As a control for these nest quadrats, the predominant vegetation type in a 0.5 m.square quadrat at 85 random points within the study area was also recorded. Observed predominant vegetation at nests was compared with that for the random quadrats.

5.2.3. Foraging habitat.

Foraging habitats selected by adults provisioning nestlings were recorded during hour-long nest watches as described in chapter 3 (see 3.2) and were assigned to one of the above categories or as unknown. Mean foraging distances for all nest visits were calculated for both males and females and were used to define a circle around the nest, the radius of which was 100 m (male mean \pm s.d.= 44.3 ± 28.5 , $n = 334$) for males and 120 m (female mean \pm s.d.= 55.2 ± 36.4 , $n = 1099$) for females. These radii included the expected 95% of foraging trips for each sex respectively, and were used to calculate expected frequencies of foraging trips to each habitat, for each nest, assuming that if there was no habitat selection the birds would visit each habitat in proportion to its availability. Areas of sea, inter-tidal zones and lochs were excluded from the analysis, as were foraging visits which could not be assigned to a habitat category. Wilcoxon signed rank tests were used to test for foraging habitat differences across nests, for males and females separately.

A potential problem with the analysis of territory habitat data in relation to chick productivity data is the non-independence between years. Five territories were occupied by the same male in both years, and six males bred in both years but moved territories between years, so it is difficult to separate territory quality from either male quality or male age/experience. The two years' data were kept separate, unless otherwise stated, so I examined similar relationships for each year.

5.3. Results

5.3.1. Nesting habitat

All nests were located on the ground; there were no bushes, trees or hedges to nest in. The distribution of nests was not random with respect to habitat category in either year, both for habitat within territories as well as habitat over the study site as a whole (1989

within territories: $\chi^2 = 19.3$, $df = 3$, $p < 0.0002$, Fig. 5.1a; 1989 whole site: $\chi^2 = 45.9$, $df = 4$, $p < 0.0001$, Fig. 5.1b; 1990 within territories: $\chi^2 = 40.9$, $df = 3$, $p < 0.0001$, Fig. 5.1c; 1990 whole site: $\chi^2 = 52.6$, $df = 4$, $p < 0.0001$, Fig. 5.1d).

In both years, within territories and overall, uncultivated land was used more often than expected for nesting. All other habitats, including cereal, were used less often than expected.

Nests tended to be situated near the coast, although this was only because the majority of uncultivated land was coastal. The nearest distances to the mean, high-water, spring tide line did not differ significantly, in either year, between nests and random points which landed in similar gross habitats to the nests (Mann-Whitney: 1989, $z = 1.95$, n (nests) = 39, n (random) = 34, $p > 0.05$; 1990, $z = 1.88$, n (nests) = 42, n (random) = 31, $p > 0.05$).

There were no differences in overall fledging success (success of all nests, including failures) between nests in different habitats when comparing cereal, fallow, marsh and uncultivated land (Kruskal-Wallis ANOVA, $H = 7.08$, $df = 3$, $p > 0.1$; Fig. 5.2).

There was no difference in the timing of breeding, as measured by corrected first egg date (cFED; See chapter 3 for definition), for nests in cereal, fallow, marsh and uncultivated land (Kruskal-Wallis ANOVA, $H = 3.70$, $df = 3$, $p < 0.5$; Fig 5.3).

In 1989, 28 of 35 nests (80%) were at the base of hogweed *Heracleum sphondylium*, yet this was the dominant plant in only 4.7% of random quadrats. Nests were significantly more likely to be at the base of hogweed than of any other plant type ($\chi^2 = 340$, $df = 1$, $p < 0.0001$; other plant types were vetch *Vicia cracca*, plantain *Plantago* spp, ragwort *Senecio jacobaea*, marram *Ammophila arenaria* and grass, Graminae).

5.3.2. Male territory habitat

Figs. 5.4 and 5.5 show the vegetation maps for 1989 and 1990 respectively. Figs. 5.6 and 5.7 are maps of the study site showing male territories, for 1989 and 1990 respectively. Although there was more fallow land, and less cereal, in 1989 than in 1990, the areas of habitat available on the study site were not significantly different, overall, between 1989 and 1990 ($\chi^2 = 7.07$, $df = 5$, $p < 0.25$; Fig. 5.8).

Fig. 5.8 shows the percentage land cover for each habitat category, for land occupied and unoccupied by male territories, for a) 1989 and b) 1990. In both years there were significant differences between habitat composition within occupied and unoccupied areas (1989: $\chi^2 = 18.1$, $df = 4$, $p < 0.001$ [marsh and 'other' grouped], Fig. 5.8a; 1990: $\chi^2 = 11.8$, $df = 4$, $p < 0.02$, [marsh and 'other' grouped], Fig. 5.8b). The greatest difference between unoccupied and occupied habitat was for pasture, which was occupied less than expected by males in both years. There was no significant difference between years for

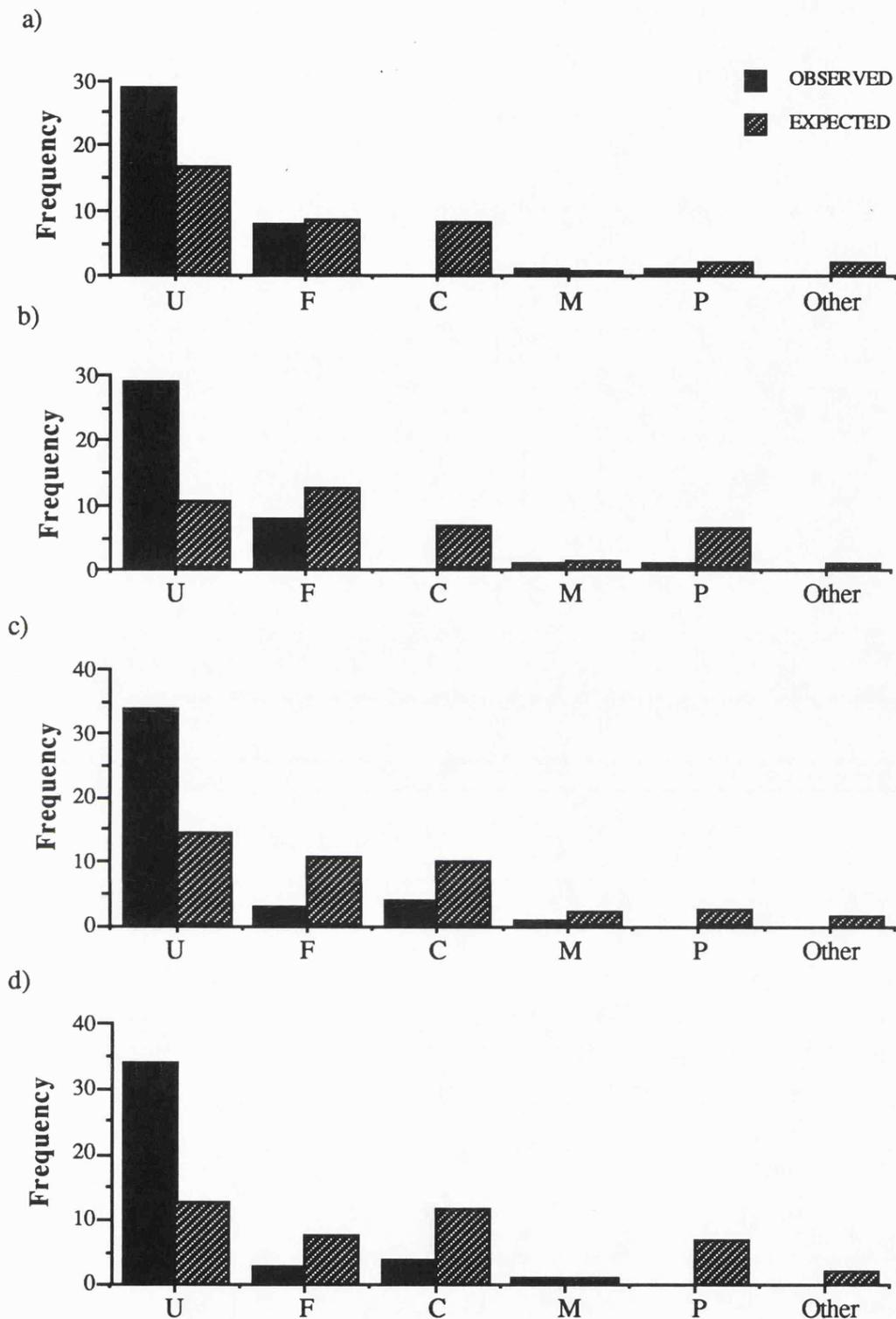


Fig. 5.1. Frequencies of nests located in each habitat category compared to that expected if females settled randomly according to habitat available within a) areas defended by males in 1989 b) the whole study area in 1989 c) areas defended by males in 1990 and d) the whole study site in 1990. In all cases there were significant differences between the observed and expected frequencies (a. $\chi^2 = 19.3$, $df = 3$, $p < 0.0002$ (M, P, Other grouped); b. $\chi^2 = 45.9$, $df = 4$, $p < 0.0001$ (M, Other grouped); c. $\chi^2 = 40.9$, $df = 3$, $p < 0.0001$ (M, P, Other grouped); d. $\chi^2 = 52.6$, $df = 4$, $p < 0.0001$ (M, Other grouped). U = uncultivated, F = fallow, C = cereal, M = marsh, P = pasture, Other = cemetery, paths/tracks, potato and hay.

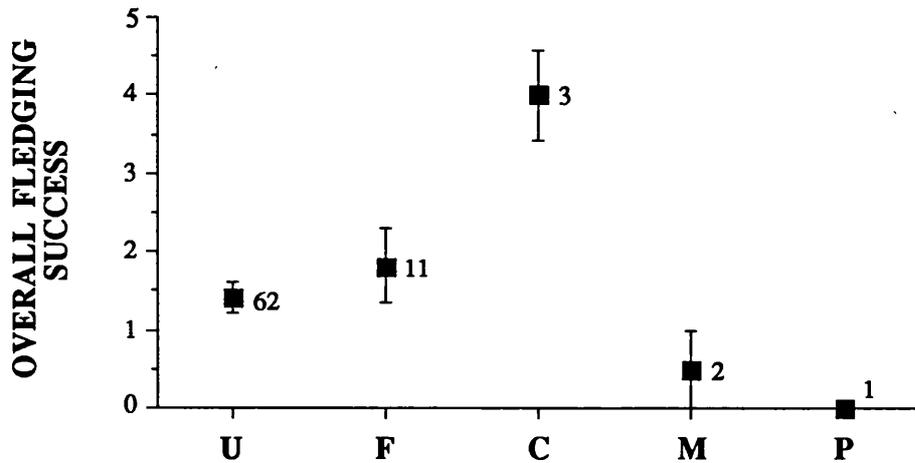


Fig. 5.2. Overall fledging success of nests in each habitat (mean \pm s.e.; U = uncultivated, F = fallow, C = cereal, M = marsh, P = pasture). There was no significant difference between the groups (Kruskal-Wallis ANOVA, $H = 7.076$, $df = 3$, $p > 0.1$; pasture omitted due to small sample size).

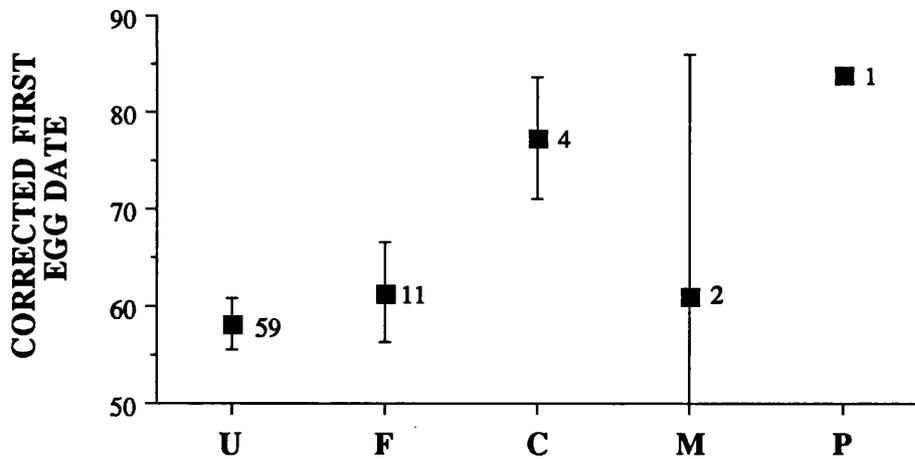


Fig. 5.3. Corrected first egg date (cFED) for nests in each habitat (mean \pm s.e.; U = uncultivated, F = fallow, C = cereal, M = marsh, P = pasture). There was no significant difference between the groups (Kruskal-Wallis ANOVA, $H = 3.698$, $df = 3$, $p < 0.5$; pasture omitted due to small sample size).

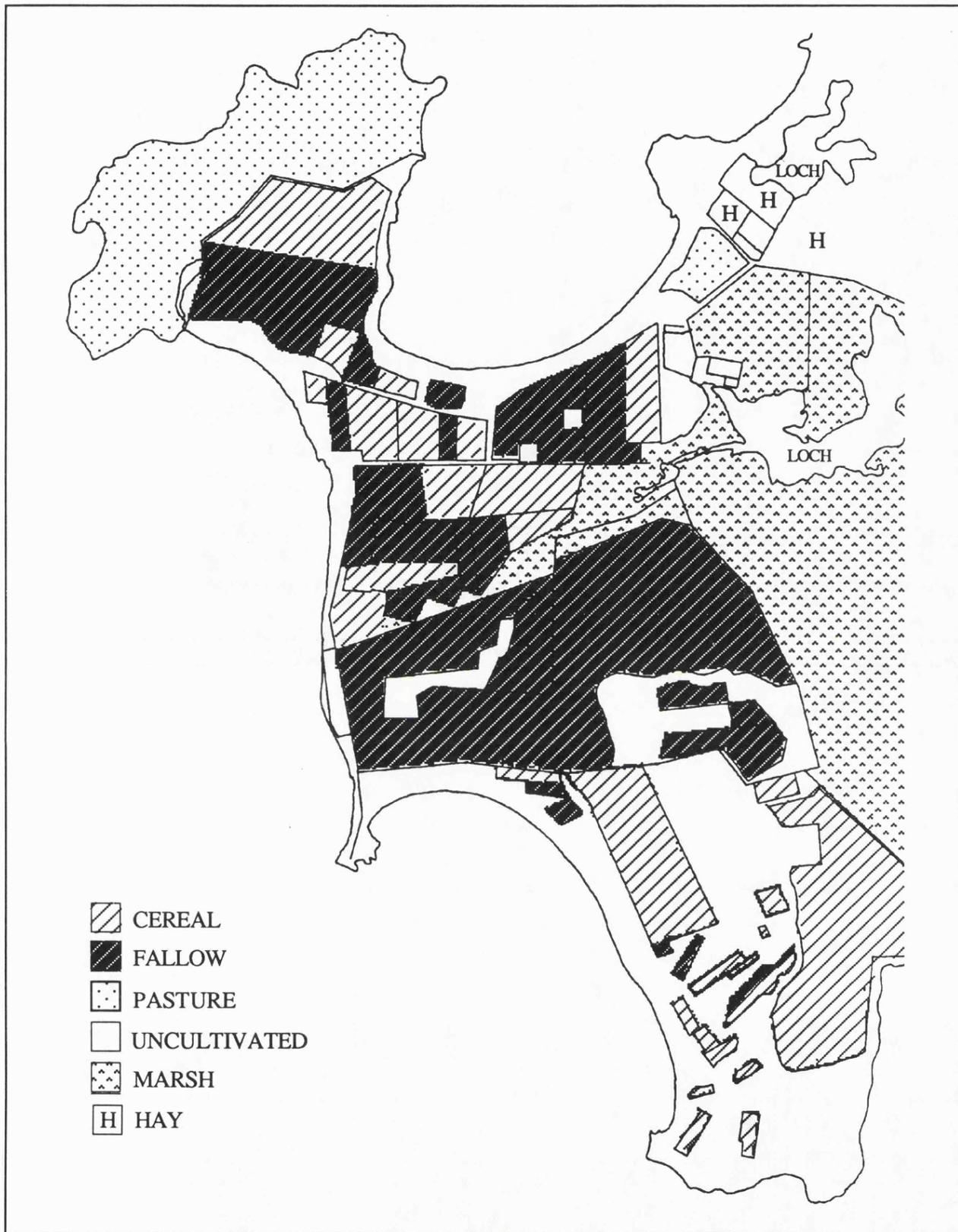


Fig. 5.4. Sketch map of habitat types on the study site in 1989

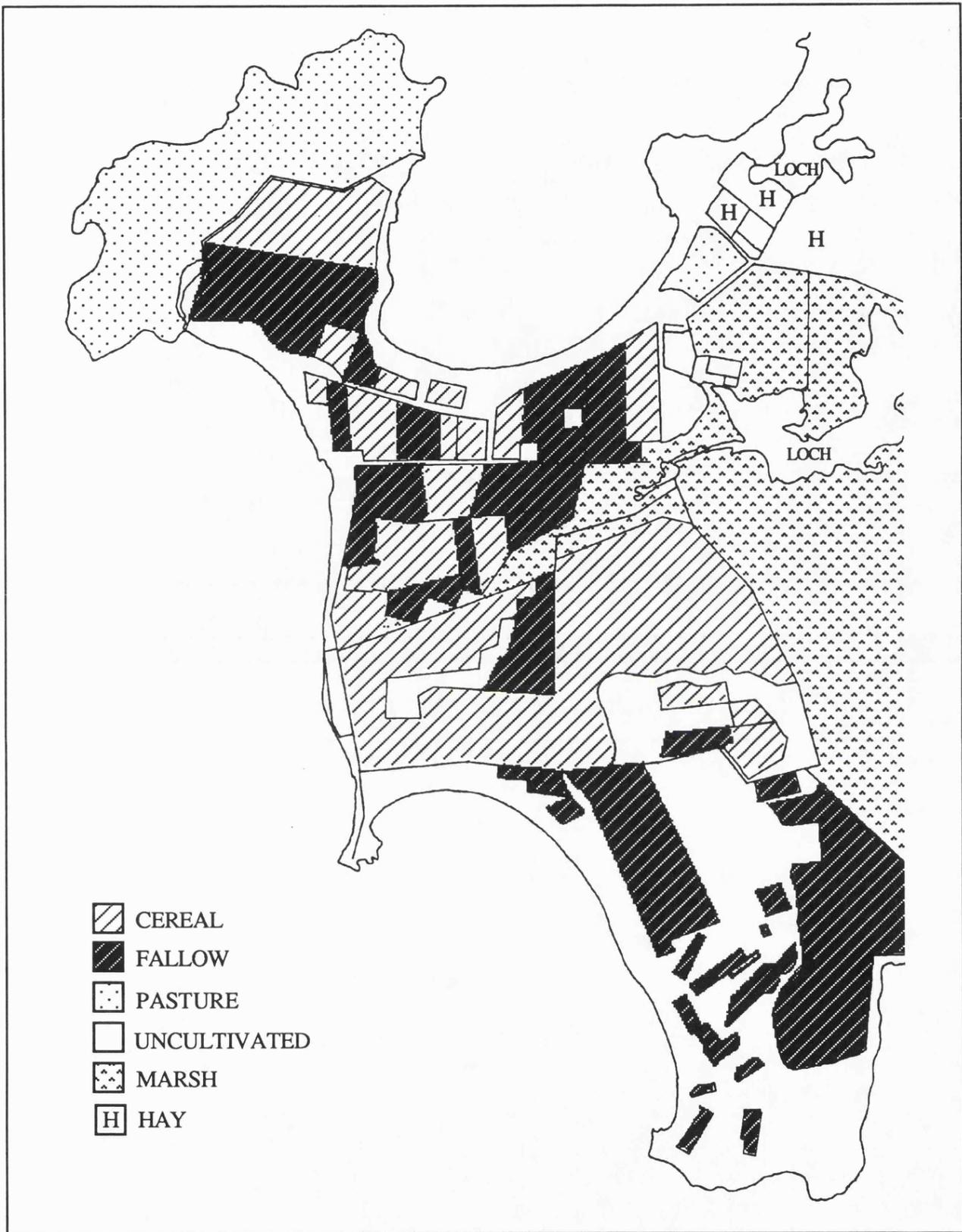


Fig. 5.5. Sketch map of habitat types on the study site in 1990

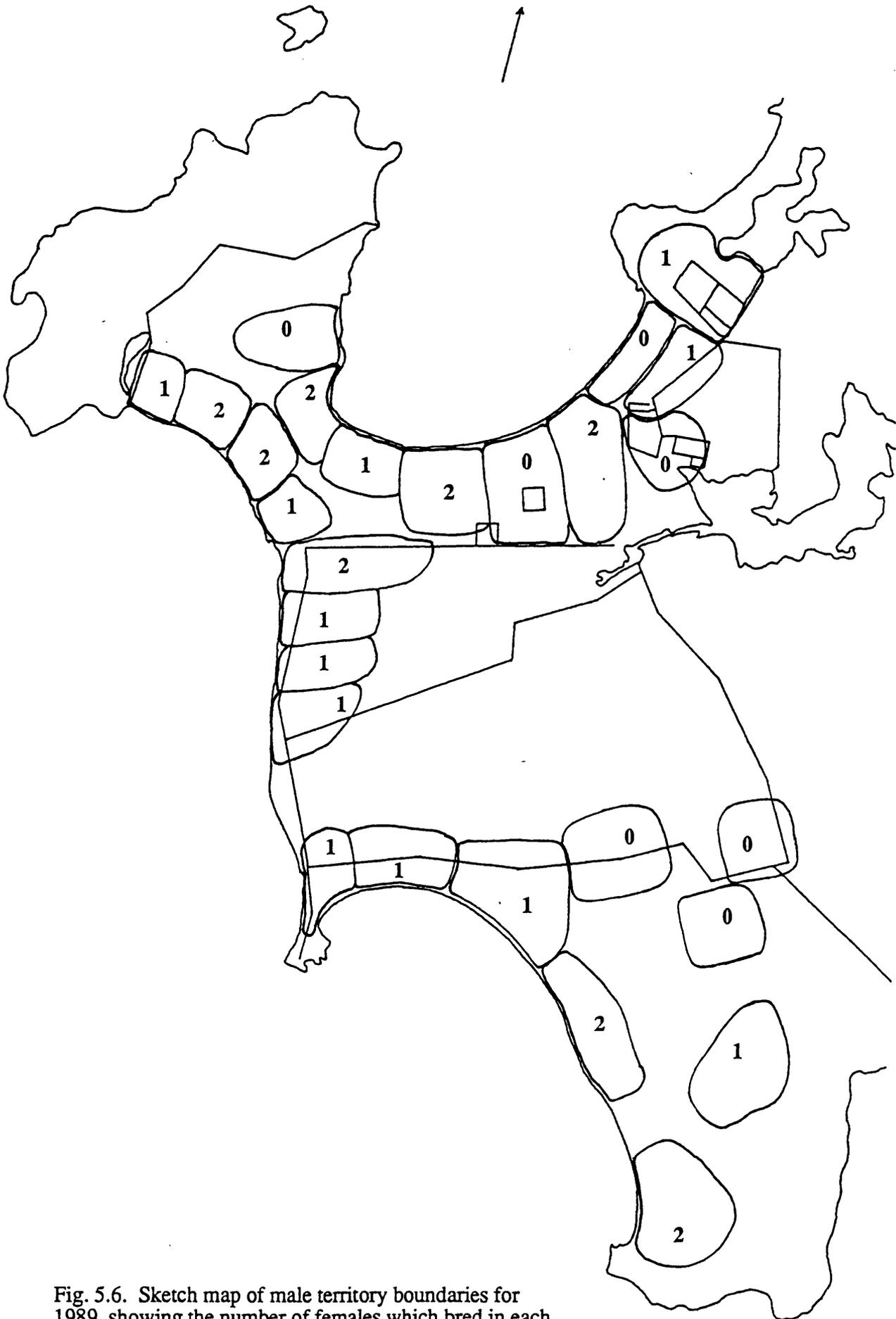


Fig. 5.6. Sketch map of male territory boundaries for 1989, showing the number of females which bred in each territory.

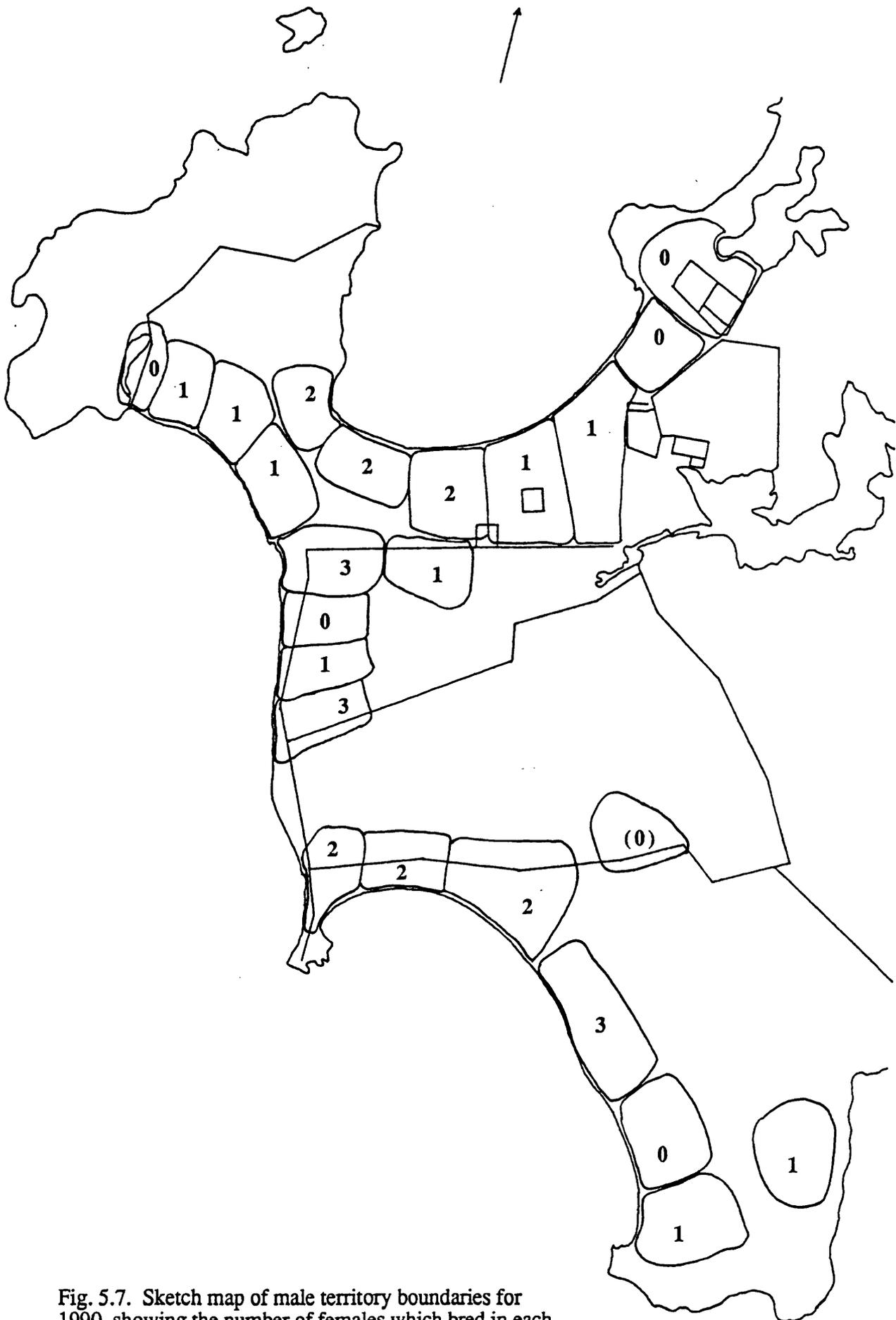


Fig. 5.7. Sketch map of male territory boundaries for 1990, showing the number of females which bred in each territory.

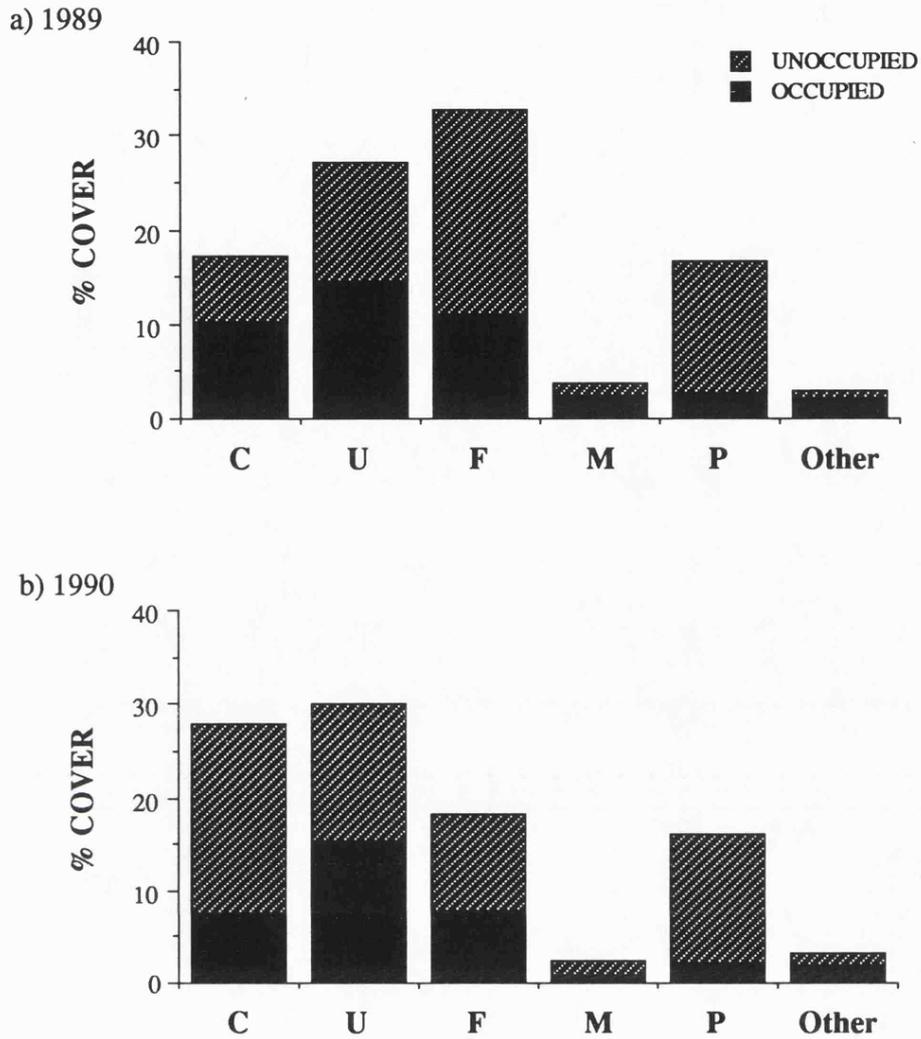


Fig. 5.8. Additive proportions of male-occupied and unoccupied land for each habitat category in a) 1989 and b) 1990. C = cereal, U = uncultivated, F = fallow, M = marsh, P = pasture, Other = cemetery, paths, potatoes and hay. The proportions of each habitat occupied and unoccupied were significantly different in both years (1989, $\chi^2 = 18.1$, $df = 4$, $p < 0.002$; 1990, $\chi^2 = 11.8$, $df = 4$, $p < 0.02$).

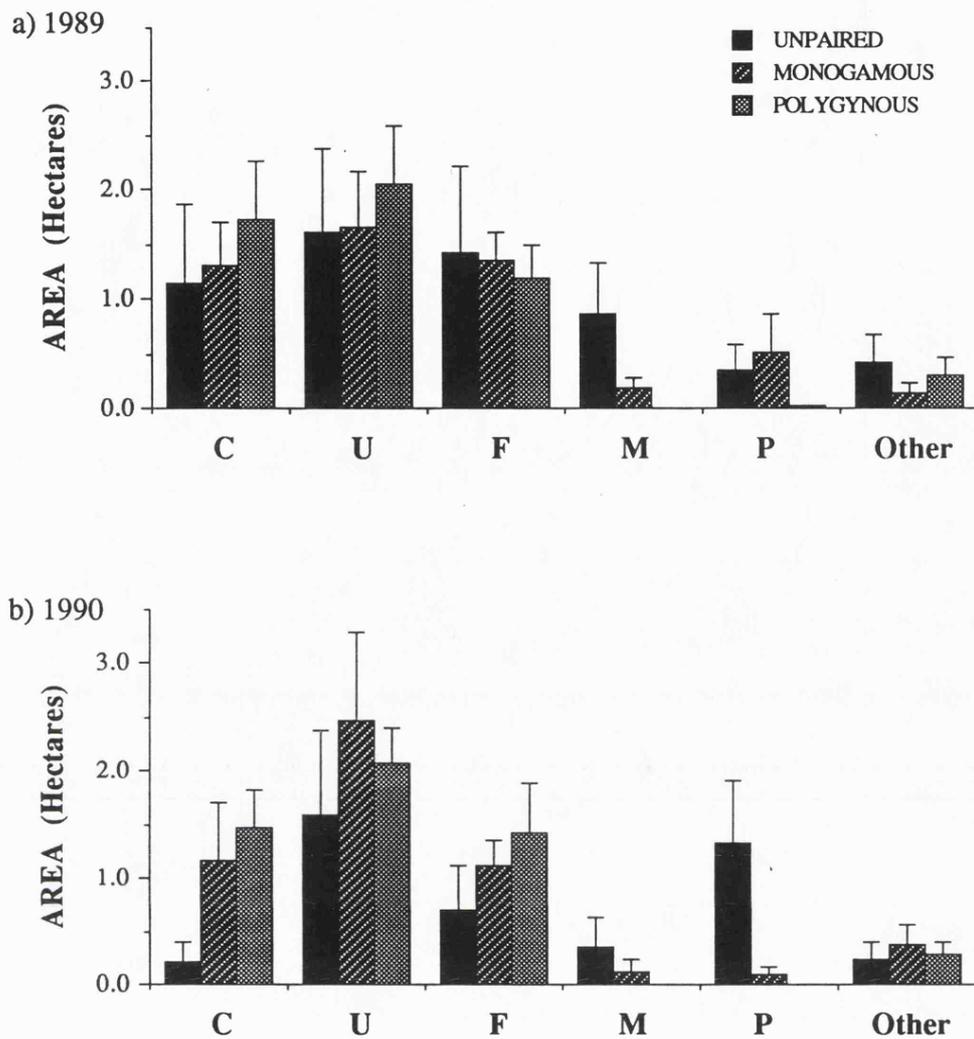
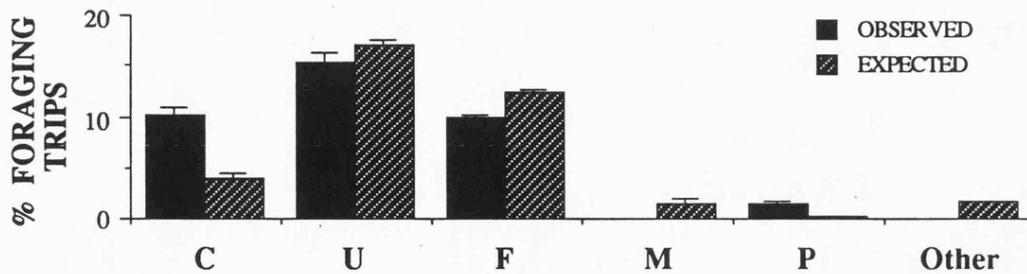
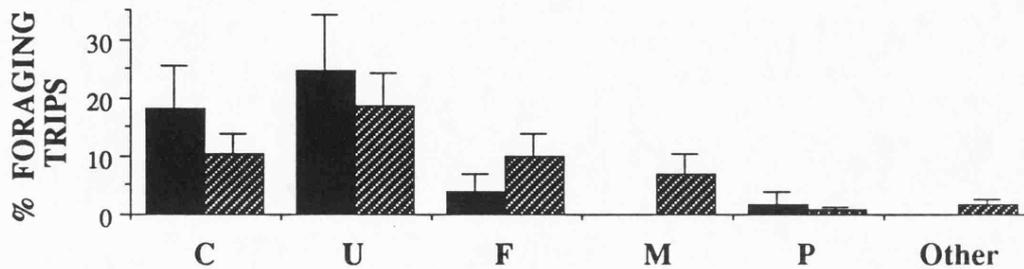


Fig. 5.9. Areas of each habitat on territories of unpaired, monogamous and polygynous males in a) 1989 and b) 1990 (mean + s.e.). C = cereal, U = uncultivated, F = fallow, M = marsh, P = pasture, Other = cemetery, paths, potatoes and hay. Kruskal-Wallis ANOVA, all $df = 2$ and N.S. ($p > 0.05$); a) 1989: Cereal $H = 2.06$; Uncultivated $H = 0.669$; Fallow $H = 0.342$; Marsh $H = 3.90$; Pasture $H = 0.669$; Other $H = 1.04$; Total area $H = 1.57$. b) 1990: Cereal $H = 5.32$; Uncultivated $H = 0.893$; Fallow $H = 0.170$; Marsh $H = 1.69$; Pasture $H = 3.96$; Other $H = 0.144$; Total area $H = 1.31$.

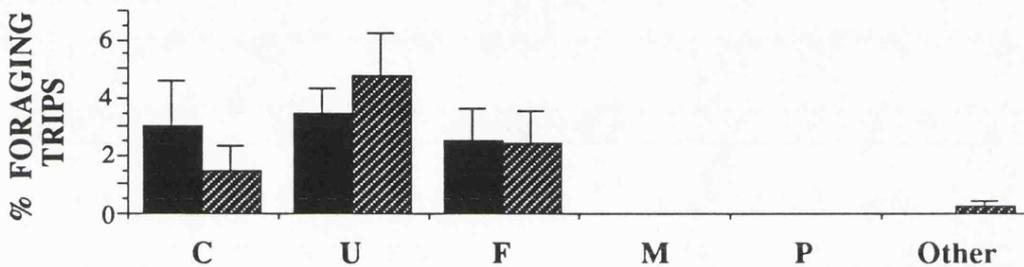
a) Females 1989.



b) Females 1990.



c) Males 1989.



d) Males 1990.

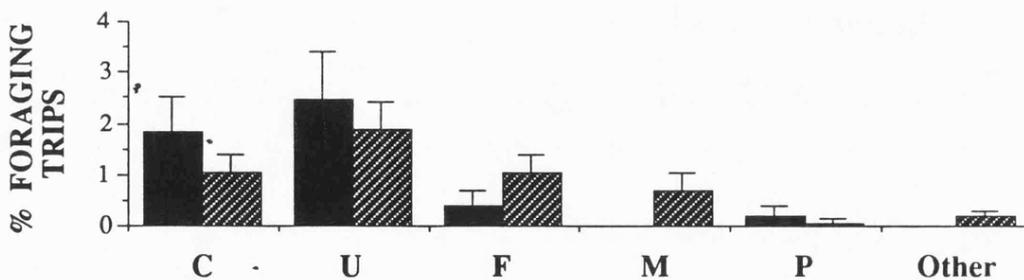


Fig. 5.10. Percentages of foraging trips observed in each habitat compared to those expected from random choice within 120m of the nest for females and 100m of the nest for males. C = cereal, U = uncultivated, F = fallow, M = marsh, P = pasture. Wilcoxon signed rank test: Fig.a) females 1989: Cereal $z = 2.01$, $N = 17$, $p < 0.05$; Uncultivated $z = 0.921$, $N = 21$, $p < 0.95$; Fallow $z = 1.17$, $N = 19$, $p < 0.25$; Marsh and pasture samples too small; Other $T = 28$, $N = 7$, $p < 0.02$. Fig. b) females 1990: Cereal $z = 3.07$, $N = 22$, $p < 0.002$; Uncultivated $z = 0.767$, $N = 25$, $p < 0.5$; Fallow $z = 2.38$, $N = 19$, $p < 0.02$; Marsh $T = 21$, $N = 6$, $p < 0.05$; Pasture sample too small; Other $T = 91$, $N = 13$, $p < 0.0002$. Fig. c) males 1989: Cereal $T = 31$, $N = 10$, $p < 0.8$; Uncultivated $T = 71$, $N = 15$, $p < 0.6$; Fallow $T = 57$, $N = 14$, $p < 0.9$; Marsh and pasture samples too small; Other $T = 15$, $N = 5$, $p < 0.1$. Fig. d) males 1990: Cereal $T = 77$, $N = 14$, $p < 0.2$; Uncultivated $T = 61$, $N = 14$, $p < 0.7$; Fallow $T = 39$, $N = 9$, $p < 0.1$; Marsh $T = 10$, $N = 4$, $p < 0.2$; Pasture sample too small; Other $T = 28$, $N = 7$, $p < 0.02$.

habitat composition within male-occupied areas ($\chi^2 = 0.941$, $df = 3$, $p < 0.9$, [marsh, pasture and 'other' grouped]), although there was a significant difference between the years for unoccupied land, as more cereal, and less fallow, was available in 1990 ($\chi^2 = 21.4$, $df = 4$, $p < 0.0005$, [marsh and 'other' grouped]).

There were no differences in either year between territories of unpaired, monogamous and polygynous males for areas of cereal, fallow, uncultivated land, pasture, marsh, or total area within male territories (For statistical tests see Fig. 5.9a,b).

In 1990 there was a significant, positive association between fledging success (fledglings per territory) and area of cereal and a significant, negative association between fledging success and pasture, and fledging success and marsh (Kendall rank correlation; Cereal $T = 0.466$, $n = 18$, $p < 0.01$; Uncultivated $T = 0.107$, $n = 18$, $p < 0.6$; Fallow $T = 0.095$, $n = 18$, $p < 0.6$; Marsh $T = -0.358$, $n = 18$, $p < 0.05$; Pasture $T = -0.474$, $n = 18$, $p < 0.01$; Other $T = 0.177$, $n = 18$, $p < 0.4$). The territory-areas of marsh and pasture were very highly correlated (Kendall rank correlation; $T = 0.724$, $n = 18$, $p < 0.0001$), but both were associated with a low number of fledglings per territory when the area of cereal on the territory was held constant (Kendall partial correlation; $T_{\text{marsh.cereal}} = -0.521$, $n = 18$, $p < 0.002$; $T_{\text{pasture.cereal}} = -0.722$, $n = 18$, $p < 0.002$). The area of cereal within territories was positively associated with the number of fledglings per territory, and this association was strengthened when areas of marsh and pasture were held constant (Kendall partial correlation; $T_{\text{cereal.marsh}} = 0.588$, $n = 18$, $p < 0.002$; $T_{\text{cereal.pasture}} = 0.719$, $n = 18$, $p < 0.002$). In 1989 there were no significant associations between fledging success and area of any habitat type within territories (Kendall rank correlation; Cereal $T = 0.158$, $n = 27$, $p < 0.25$; Uncultivated $T = 0.099$, $n = 27$, $p < 0.5$; Fallow $T = 0.124$, $n = 27$, $p < 0.4$; Marsh $T = -0.153$, $n = 27$, $p < 0.3$; Pasture $T = -0.249$, $n = 27$, $p < 0.1$; Other $T = 0.100$, $n = 27$, $p < 0.5$).

For territories occupied in 1989 and/or 1990 there was a significant association between the years for the number of nesting females on each territory ($r_s = 0.529$, $n = 29$, $p < 0.005$), as would be expected if high quality territories held more nesting females and male quality could be held constant for age, experience and other factors. Eleven males held territories in both years (1989 $n = 26$ territories, 1990 $n = 24$ territories), of which five held the same territory and six switched territories. Of the five males that switched territories between years, four paired with more nesting females than the previous year and one was monogamous in both years, although the numbers are too small for a meaningful analysis.

5.3.3. Foraging habitat

When female corn buntings were provisioning nestlings they foraged more often than expected in cereal in both 1989 and 1990 (for statistical tests see Fig. 5.10a,b). In 1990 females were recorded foraging significantly less often than expected in fallow and marsh,

and there was no significant difference between observed and expected foraging frequencies for uncultivated habitat (for statistical tests see Fig. 5.10b). In 1989 females showed no significant differences between observed and expected foraging frequencies in fallow, pasture or uncultivated habitat categories (for statistical tests see Fig. 5.10a). In both years females foraged significantly less often than expected in 'other' habitat (paths, the cemetery, potato patches and hay) (for statistical tests see Fig. 5.10b).

Males did not show significant differences between observed and expected foraging habitat in either year for cereal, fallow, marsh, uncultivated or pasture habitats, and 'other' land in 1989 (For statistical tests see Fig. 5.10c, d). In 1990 males foraged significantly less than expected in 'other' habitats (paths, the cemetery, potato patches and hay) (for statistical test see Fig. 5.10d).

5.4. Discussion

5.4.1. Habitat and polygyny

Females selected uncultivated land as nesting habitat and chose to nest under hogweed in preference to other plants. They often foraged outside the male territory and significantly preferred to forage in cereal in both years. Male territory boundaries were similar in both years despite a considerable change in the position of the main cereal area on the study site. It seems, therefore, that males defended areas which provided good nest sites, rather than good foraging grounds, for females. The only habitat consistently avoided was pasture, much of which was grazed short by cattle and sheep, and so provided no nesting cover. In 1990 there was a negative correlation between the areas of pasture and marsh on territories and the number of fledglings per territory, reflecting the fact that both of these habitats were avoided for nest building. In 1990, but not in 1989, there was a strong positive correlation between area of cereal within territories and the number of fledglings per territory, which is further evidence that cereal may be important for fledging young, although it is not fully conclusive.

Females preferred to build their nests at the base of hogweed (as opposed to marram or cereal as has previously been suggested for Uist corn buntings [Williams *et al.* 1986]), probably because it provided good nesting cover from predators and against wet and windy weather. Hogweed has broad leaves which cover much of the ground, while at the same time allowing room at the stem bases for nests to be built. Later in the season cereal could also provide cover for nests and although there was no significant difference between nest sites for timing of breeding, the few nests that were in cereal were late ones. This probably does not reflect a switch in preference, but more likely a new habitat (for that season) that can be used when available but which is not available earlier. Nests built in cereals may lack the overhead cover from rain and predators that is provided by hogweed.

There is no evidence to suggest that nests in different habitats have different success

rates but, as most nests are in hogweed on uncultivated land anyway, there is little to compare them with, without experimentally pruning nesting vegetation.

If the polygyny threshold model can be used to explain polygyny in the corn bunting, then one should expect a relationship between the paired status of the male and the relevant, important habitat parameter. This was not found from the data above. Unpaired, monogamous and polygynous males were not significantly different for any measured areas of habitat categories within their territories. There was, however, a significant correlation between the numbers of females nesting on each territory between years, suggesting that there are real differences between territories but that the original habitat data collection may not have been on a fine enough scale to detect it. This analysis does not control for male age between the years but it does, however, suggest that territories which were 'good' for females in 1989 were also 'good' for them in 1990. Males should not be expected to change the overall pattern of territory tenure over the study site, as crops are rotated with fallow areas, because females select territories for the nesting habitat, which is mainly on uncultivated land. Males take up territories in March and April, when cereals have not yet been planted nor the fallow ploughed, but they do not rearrange their space defence later in the season, to occupy areas of cereal or fallow, despite the fact that they would have time to do so before females settled to breed. Perhaps males stay on their original territories within a season because moving to a new area and attempting to usurp a resident male would be too costly.

5.4.2. The national corn bunting decline and habitat change

In other areas of Britain, where the corn bunting is generally declining, agricultural practices are more intense than on North Uist. Two main reasons have been put forward to explain the decline of the corn bunting elsewhere in Britain:-

- 1) loss of feeding habitat as a result of a decline in barley growing (Thompson and Gribbin 1986).

- 2) loss of breeding habitat as a result of intensification of arable farming and the consequent increase in herbicides at field margins (O'Connor and Shrubbs 1986).

Both of these factors probably play a part in reducing overall populations of corn buntings, as this study has shown habitat to be important for both food and nesting habitat in different ways. Although females in this study preferred to nest in hogweed, and seemed to avoid cereal, other studies have found variable nesting habitat preferences, with some finding a preference for cereal (Goodbody 1985; MacDonald 1965), whereas others found that cereals were avoided (Ryves and Ryves 1934a,b; Walpole-Bond 1938; Møller 1983). In Switzerland corn buntings nested in marshes and wet areas but avoided crops (Hegelbach and Ziswiler 1979). It may be that recent changes in agricultural practices have forced the corn bunting to nest in cereal crops in line with a reduction in area of field

margins and other preferred nesting habitat.

It is difficult to extrapolate the results from this study to other agricultural areas of Britain, however, as the Uists are farmed in a very low intensity way with no use of pesticides, absence of large fields and crude harvesting machinery. One change in farming practice, which may reduce the suitability of North Uist for corn buntings, is the increased use of bagged and buried silage for winter cattle feed. The traditional alternative is to store cropped cereal in stooks in enclosures, which are fully accessible to corn bunting flocks. In winter nearly all corn buntings and other small passerines aggregate to feed around such stooks or where feed is laid out for cattle (pers. obs.). When silage is bagged and buried in sand pits, not only is the main food source removed from access to the birds, but it is cropped before it fully goes to seed and so reduces spillage on the land. As mortality of adults is low in summer (1 or 2 adults per breeding season), it is possible that food availability in winter may be critical to their survival.

5.5. Summary

1) The effects of habitat on the settling patterns of female corn buntings were investigated to determine if females chose territories according to nest site quality, foraging areas or neither. If the variance in male territory quality is high, the polygyny threshold model for the evolution of polygyny predicts that females should have a higher fitness with an already paired male in a high quality breeding situation than they would if they paired monogamously to an unpaired male.

2) Female corn buntings nest at the base of hogweed on uncultivated land in preference to other habitats and females provisioning nestlings prefer to forage in cereals rather than other habitats, although males do not show a similar preference. Females often foraged outside male territories. Males appeared to defend areas in which females chose to nest rather than to forage.

3) The territories of unpaired, monogamous and polygynous males did not differ significantly in habitat composition. There was, however, some evidence to show that territories were consistent between years for the number of females settling, despite a change of males. This suggests that some territories may have been more attractive than others.

4) Females may settle randomly within certain limits, such as nesting in hogweed, so that male territories are not variable enough to account for the levels of polygyny described in chapter 2.

5) The national decline in corn bunting numbers since the 1950s has been linked to a reduction in the growth of barley. This association may well only be correlational, however, and probably reflects a general intensification of agricultural practices which

includes increased use of pesticides, field margin removal and faster turnover of harvested land back to plough; all of which reduce nesting and foraging areas for corn buntings. Winter food sources may also prove to be an important factor in the decline.

Chapter 6. A review of polygyny models and polygyny in the corn bunting

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6.2.2. The polygyny threshold model (PTM)

6.2.3. The deception hypothesis

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6.3. Polygyny in corn buntings

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6.5. Results

6.5.1. Nest dispersion in space and time

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6.6. Discussion

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6.6.2. Nesting dispersion in time

6.6.3. Female settlement within male territories

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6.7. Conclusion

6.8. Summary

6.1. Introduction

In birds, polygyny usually centres on territories rather than on male coercion of harems, with males defending an area, or areas, within which females nest and raise young. Much interest, in the past 25 years, has centred around the relative occurrences of polygyny and monogamy, and their costs and benefits to each sex. Several explanations for polygyny have been proposed, which have been discussed, tested to various degrees and applied to a range of species with varying ecology. Much of this work has been connected with one of several models: the polygyny threshold model (PTM) (Verner 1964; Verner and Willson 1966; Orians 1969), the deception hypothesis (Alatalo *et al.* 1981), the sexy-son hypothesis (Weatherhead and Robertson 1979, 1981) and the neutral mate choice

hypothesis (Lightbody and Weatherhead 1988).

Recently, Searcy and Yasukawa (1989) proposed a hierarchical classification of polygyny models which included all the current theories and sorted them into testable and workable groupings. They pointed out that whilst many workers continued to test particular models, a more productive approach would be to identify the most appropriate model for the species under study.

This chapter reviews the current state of polygyny models, then applies Searcy and Yasukawa's (1989) hierarchical classification approach to finding the nearest fitting model which explains the maintenance of polygyny in the corn bunting.

6.2. The current state of polygyny models

6.2.1. Model classification

Fig. 6.1 shows an adaptation of Searcy and Yasukawa's (1989) hierarchical classification of polygyny models.

Models are firstly divided into 'male-coercion' or 'female-choice' models. All current models of territorial polygyny in birds are based on female choice rather than direct male coercion or harem defence polygyny (Emlen and Oring 1977). It is difficult to see how a male could actually prevent a female from leaving his territory, let alone force her to breed there. Male coercion (Searcy and Yasukawa 1989) or harem defence polygyny, as Emlen and Oring (1977) call it, has not been recorded in passerine birds (Garson *et al.* 1981).

Within the female-choice grouping the next division is between 'cost' and 'no-cost' models, based on the net costs incurred by females which pair polygynously as opposed to monogamously. No-cost models are either positive gain models, where female reproductive success increases with increasing harem size, or neutral gain models, where female reproductive success shows no relationship with harem size. In either case, models can be classified further into those in which females choose males according to the quality of the breeding situation or choose males according to male quality (i.e., at random with respect to the quality of the breeding situation).

Most current models are based on the theory that polygyny is costly to females. There are two categories of female cost models: those in which the sex-ratio is skewed towards an excess of females so that some females must pair polygynously in order to breed, and those models where the sex ratio is balanced, but some females choose to pair polygynously, leaving unmated males available. Balanced sex ratio models are further divided. Compensation models (e.g., the PTM [Verner and Willson 1966; Orians 1969]) are those in which the costs to females of pairing polygynously are compensated for by access to superior breeding situations. No-compensation models are those in which females are not compensated for the cost of polygyny but pair polygynously because:-

- 1) The cost of searching for an unpaired male is prohibitively high.

1. **Male coercion** - unlikely in territorially polygynous birds.

2. **Female choice** -

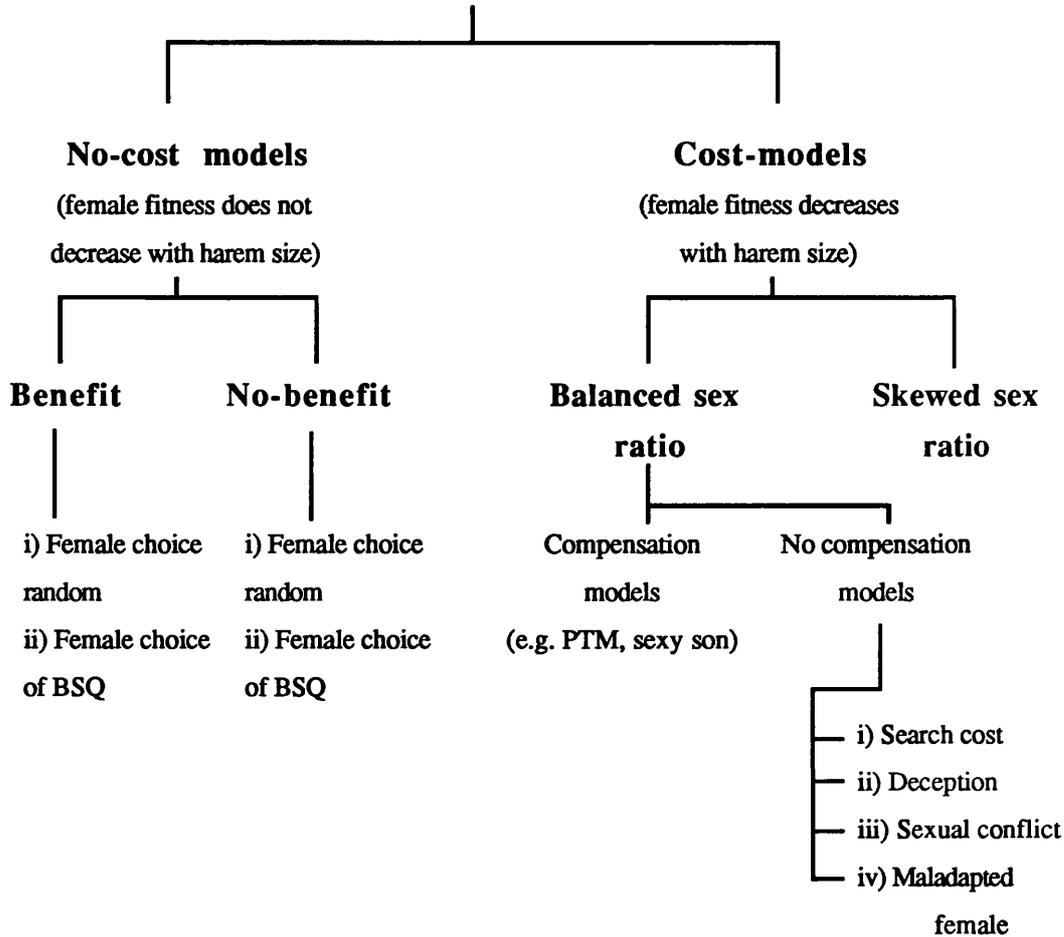


Fig. 6.1. Hierarchical classification of models of polygyny in territorial birds. (Adapted from Searcy and Yasukawa 1989). BSQ = breeding situation quality; PTM = polygyny threshold model.

2) Females are 'deceived' into pairing polygynously because they 'think' that a male is unpaired.

3) Females know the male is already paired, but choose to pair polygynously despite the possibilities of better pay-offs elsewhere (the 'maladapted female' model [Searcy and Yasukawa 1989]).

4) Two females, competing for a male territory which neither can monopolize, have to share the male (Davies 1989).

I now describe each model in detail.

6.2.2. The polygyny threshold model (PTM)

The PTM (Verner 1964; Verner and Willson 1966; Orians 1969) is probably the most tested and discussed model of polygyny to date (Zimmerman 1966; Martin 1974; Wittenberger 1976, 1979; Altmann *et al.* 1977; Pleszczynska 1978; Carey and Nolan 1975, 1979; Pleszczynska and Hansell 1980; Lenington 1980; Garson *et al.* 1981; Gowaty 1981; Wootton *et al.* 1986; Yasukawa and Searcy 1986; Dhondt 1987; Leonard 1990; Bensch and Hasselquist in press). So far, however, fully convincing evidence supporting the model is lacking (Vehrencamp and Bradbury 1984; Davies 1989). The original model (Verner 1964; Verner and Willson 1966; Orians 1969) predicts that females should pair polygynously if the variance in quality of male territories is so great that a female could achieve higher fitness by sharing resources with the female(s) of an already paired male rather than by pairing with an unpaired male. The original Verner and Willson (1966) and Orians (1969) models used territory quality as the measure of breeding situation quality but it is now accepted that this should be expanded to include quality of nest sites, foraging sites, male parental care and genetic benefits (Altmann *et al.* 1977; Wittenberger 1979; Gowaty 1981; Weatherhead and Robertson 1979, 1981).

The PTM has four main assumptions (Orians 1969; Garson *et al.* 1981; Davies 1989):-

1) Males vary in the quality of a defended resource which influences female reproductive success.

2) There is a cost to females of sharing a breeding situation with other females.

3) Females can assess the quality of the breeding situation and male paired status perfectly.

4) Females can freely choose where they breed, and choose so as to maximize their fitness.

The PTM is illustrated by a function curve of female fitness against the quality of the breeding situation (Fig. 6.2). Curves for females which are the first to settle on a territory and subsequent females are shown separately because, in the simplest form of the PTM, a female settling as the secondary female is predicted to have lower fitness than the male's primary female (Garson *et al.* 1981). Subsequently settling females are predicted to have

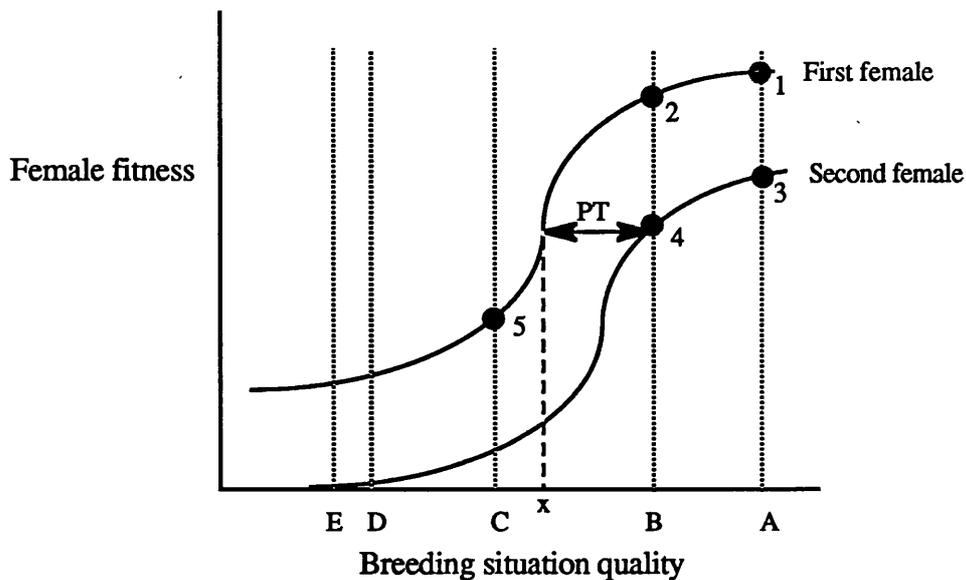


Fig. 6.2. Function curves for primary and secondary females settling according to the polygyny threshold model. A to E represent males offering specific qualities of breeding situations which affect female fitness, with A offering the highest fitness return and E the lowest. The filled circles (●) represent the fitness expected for females settling with specific males as either the first or second female. The best settling option is '1', the second best '2' and so on, and females are expected to settle in the order 1 to 5, which would result in males A and B being bigamous, C monogamous and D and E unpaired. PT is the 'polygyny threshold', which represents the difference in breeding situation quality which is needed to make polygyny a better option than monogamy. As $C < X$ for quality of breeding situation, the best option of the fourth female to settle is to pair polygynously with male B, rather than monogamously with male C. The best option available to the fifth female to settle is monogamy with male C.

This is a simplified version of the PTM and other factors, such as nest predation, timing of breeding and effects of the later settling females on the primary female, are discussed in the text.

Adapted from Orians (1969).

decreasing fitness as they settle in situations with decreasing quality. The curve is S-shaped because females need a certain level of resources to breed but can utilize only a finite amount of those available.

In a simple interpretation of the PTM (Fig. 6.2), there are five male territories and five settling females. The function curves predict the pay-offs to females of each status nesting on those territories. Fig. 6.2 assumes that primary settling females receive a preferential share of the available resources (as in Garson *et al.* 1981) rather than an equal share with subsequently settling females (Davies 1989). The five females should settle in the best option remaining available to them, in this case in the sites marked 1-5. This would result in males A and B being bigamous, C being monogamous and D and E remaining unpaired. The horizontal distance between the curves is called the polygyny threshold (PT) because this is the required difference between the quality of two breeding situations which could return equal fitness to the primary female on one territory and the secondary (or subsequent) female on another; quality differences greater than the PT should induce polygyny.

In an extreme case, the polygyny threshold may be so great that being a secondary female could never pay, in which case monogamy would be the norm. Alternatively, the threshold could be so small that the costs of polygyny to females are relatively cheap, thus facilitating polygyny. For example, the polygyny threshold could be reduced by:-

- 1) Nesting asynchrony within territories because females would not compete for resources at critical periods (Leonard and Picman 1987; Derrickson 1989; Leonard 1990).

- 2) A high risk of nest predation, which means that there would be a high chance of a secondary female attaining primary status if the original primary female's nest is predated, so forcing her to reneest (Temrin and Jakobsson 1988; Urano 1990; Bensch and Hasselquist in press).

In Searcy and Yasukawa's (1989) classification of polygyny models the PTM is a compensation model because although pairing polygynously is costly to females, they are compensated with access to a better breeding situation than if they paired monogamously with the next available unpaired male.

Although there have been many attempts to test the PTM, many have failed to address the assumptions of the model properly and have therefore applied it inappropriately (Altmann *et al.* 1977; Vehrencamp and Bradbury 1984; Davies 1989). Vehrencamp and Bradbury (1984) pointed out that most tests either concentrate on only a few components of fitness, such as the number of chicks fledged, or they have made invalid assumptions to short-cut the test. They suggest that a proper interpretation of the PTM predicts that male rank for the critical resource should correlate with:-

- 1) Final harem size, because male resource holding potential should correlate with resource utilization by females.

2) The order of settlement of the 1st, 2nd, etc. females to settle, because females are expected to settle according to their best available option at the time; the best breeding situations will be occupied first by primary females and subsequently settling females should settle in the same order.

3) The rank of fitness of the 1st, 2nd, etc. females to settle in similar sized harems, because in such cases the effects of other females (competition for resources) should be similar, yet females settle on territories in order of decreasing quality of the breeding situation.

The prediction that monogamous and secondary females, settling at the same time, should have the same reproductive success is unnecessary (Altmann *et al.* 1977; Vehrencamp and Bradbury 1984) because the model is based on rank orders rather than absolute values of reproductive success, and the differences in fitness between females settling at the same time are dependent upon the shape of the function curves in Fig. 6.2. The prediction that earlier settling females should have a higher reproductive success than later settling females is also unnecessary, because this prediction depends heavily on how resources are shared between females on the same territory (Altmann *et al.* 1977). For example, if all resources are divided equally between females on a territory, it is possible for later settling females to reduce the first settling females' share to below that of females on the second best territory (Vehrencamp and Bradbury 1984).

Identification of critical resources, which affect reproductive success, and components of fitness, which are affected by polygyny, is probably impossible (Vehrencamp and Bradbury 1984) and so the PTM has remained largely untested, despite many attempts.

6.2.3. The deception and search cost hypotheses

The deception hypothesis (Alatalo *et al.* 1981) is a non-compensation model which suggests that settling females cannot tell whether or not a male is already paired and secondary and subsequent females are not compensated for the costs of polygyny.

Males could hide their true paired status in two ways: 1) polyterritoriality, where a male holds two or more spatially separated territories, so that a secondary settling female does not see the primary female (e.g., pied flycatchers [Alatalo *et al.* 1981, 1982] and wood warblers [Temrin and Jakobsson 1988; Gyllensten *et al.* 1990]) or 2) the occupation of low visibility habitats, such as reed beds, could allow males to pair polygynously without the knowledge of his females (as suggested for great reed warblers [Catchpole *et al.* 1985]).

In these species secondary and subsequent females usually have a lower fitness than primary and monogamous females because males provide the primary females with more incubation feeds (Lifjeld and Slagsvold 1986; Lifjeld *et al.* 1987) and parental care (Alatalo *et al.* 1981, 1982; Lifjeld and Slagsvold 1990; Urano 1990; Bensch and Hasselquist in

press).

Alatalo *et al.* (1981, 1982, 1984a, 1991) and Alatalo and Lundberg (1984) proposed the hypothesis as an explanation for polygyny in the polyterritorial pied flycatcher, although Stenmark *et al.* (1988) and Breihagen and Slagsvold (1988) have argued that females should be able to tell whether a male is already paired or not from his behaviour. They found that male behaviour was different on secondary territories in comparison with primary territories because they divided their time between the two, and also that primary females have been seen to be aggressive towards secondary females on the secondary territory (Breihagen and Slagsvold 1988). More recent evidence shows that males spend more time on a secondary territory after the arrival of a female (Searcy *et al.* 1991), although the authors admit that the deception hypothesis cannot be convincingly tested because it would never be known whether a female actually knew whether or not the male was paired.

An alternative to the deception hypothesis is the search cost hypothesis (Breihagen and Slagsvold 1988; Stenmark *et al.* 1988; Slagsvold *et al.* 1988; Searcy and Yasukawa 1989; Dale *et al.* 1990), which proposes that females could do better by pairing with an unpaired male but do not have time to find one, as reproductive success declines with the short breeding season.

No test of either hypothesis has shown that females do not know if an unpaired male is available when they settle. If females can be shown to have visited unpaired males prior to settling with a paired male on his secondary territory, the search cost hypothesis will not be supported, although the deception hypothesis would not be refuted. As Searcy *et al.* (1991) point out, the argument hinges on whether or not females could 'know' if a male was paired and, more importantly, whether researchers could tell if a female 'thought' her male was unpaired when in fact he was not.

6.2.4. The 'sexy son' hypothesis

Originally, the 'sexy son' hypothesis (Weatherhead and Robertson 1979, 1981) was put forward to explain the reduction of the polygyny threshold in terms of the secondary sexual characteristics of males. The model is an extension of Fisher's runaway theory of sexual selection (Fisher 1930) and suggested that females paired with the most attractive males so that their sons were also attractive and therefore polygynous when they came to breed. Any reduction in immediate female fitness as a result of pairing polygynously is compensated for by the longer term genetic gain from her son (Weatherhead and Robertson 1979, 1981).

Theoretical work did not support the 'sexy son' hypothesis (Wittenberger 1981; Heisler 1981; Searcy and Yasukawa 1981; Kirkpatrick 1985), although more recent models suggest that sexual selection could (in theory) favour females choosing males to

father 'sexy sons' if the cost of choosing those males was not too high, or in other words if the polygyny threshold was very low (Pomiankowski *et al.* 1991; Iwasa *et al.* 1991). The relevance of the 'sexy son' in sexual selection and polygyny may be more appropriate in lekking, rather than in territorially polygynous species, as in such cases the male only supplies gametes to the female who would not, therefore, suffer costs through having to share male resources other than sperm. Current empirical evidence does not support the hypothesis that 'sexy son' benefits reduce the polygyny threshold in territorial polygynists (Alatalo and Lundberg 1986). In pied flycatchers it was found that heritability of male pairing success was low (Alatalo *et al.* 1981; Alatalo and Lundberg 1986; but see Hedrick 1988 for an alternative in a cricket, *Gryllus integer*), and sons of secondary females were of lower phenotypic quality than sons of monogamous or primary females because they received less paternal care (Alatalo *et al.* 1982; Alatalo and Lundberg 1984, 1986b). There is also strong evidence to suggest that females settle according to the quality of nest sites rather than the phenotypic characters of males (Alatalo *et al.* 1986b; Askenmo 1984; Slagsvold 1986), although in pied flycatchers, models of polygyny other than compensation models may apply.

6.2.5. Neutral mate choice hypothesis

The neutral mate choice hypothesis predicts that polygyny is neither costly nor beneficial to females and consequently harem size is not related to female reproductive success (Lightbody and Weatherhead 1987, 1988). This is not quite the same as a random settlement model because females are expected to behave optimally under the neutral mate choice hypothesis, rather than settling independently of breeding situation quality and other females, which could lead to suboptimal settlement (Lightbody and Weatherhead 1988). According to Searcy and Yasukawa's (1989) classification, this model could be a no-benefit or benefit model in the no-cost category (Fig. 6.1).

The model was designed around the mating system of the polygynous yellow-headed blackbird, a species in which males take little or no part in parental care (Lightbody and Weatherhead 1987, 1988). One of the predictions of the model is that harem size should increase with increasing territory size because larger territories could provide more nest sites for females. Male-male competition for territories decides which males obtain the most females and male yellow-headed blackbirds with the largest territories do indeed obtain the most females (Lightbody and Weatherhead 1988).

6.3. Polygyny in corn buntings

As one would expect for a species in which males defend territories rather than harems (Emlen and Oring 1977; Searcy and Yasukawa 1989), male coercion did not appear to determine where a female nested. Female reproductive success is similar across secondary

and primary females, but monogamous females are less successful (chapter 3), so it appears that females do not suffer (and indeed may benefit) from reduced annual reproductive success through pairing polygynously. It is necessary to determine whether polygyny is costly to females, but fully compensated, or not costly at all. One way of differentiating cost and no-cost models is to determine the costs and benefits which affect female reproductive success and correlate the net cost against female pairing status (Searcy and Yasukawa 1989). It has been shown previously (chapter 4) that males feed nestlings of monogamous, primary and secondary females at similar rates, and that males of different pairing status did not obviously differ for territory features important to females, such as nesting habitat (chapter 5). These observations suggest that polygyny is not costly to females. However, if female settlement is influenced by access to resources, and females are fully compensated for the costs of polygyny, they should settle according to the PTM.

The assumptions of the PTM are listed in 6.2.2. Male corn buntings did not differ in the defended resource measured (nest site availability; chapter 5), which influenced females reproductive success, but it is difficult to measure every aspect of breeding situation quality and the true critical features may not have been measured (chapter 5). If there is a cost to females of sharing territories with other females one should expect nests to be over-dispersed in space and/or time (e.g., Leonard and Picman 1987; Leonard 1990). One should also expect females to behave aggressively towards one another (Holm 1973; Lenington 1980; Yasukawa and Searcy 1982; Hurley and Robertson 1984; Davies 1985; Leonard and Picman 1987; Stenmark *et al.* 1988). Females were probably free to choose where to nest, as males seemed unable to force them to nest in particular areas (Emlen and Oring 1977; Searcy and Yasukawa 1989). The assumption that females have perfect knowledge of male status and quality of the breeding situation needs to be tested experimentally and remains an assumption here.

The following predictions would have to be met to support the PTM, rather than a no-cost model of polygyny:

1) Nests are over-dispersed in space and/or time due to female competition for resources.

2) Female settlement order is positively correlated with the quality of the breeding situation, so that primary females settle on territories in the same order as the corresponding secondary females.

3) Harem size should be negatively correlated with settlement date of the first female on a territory because the best breeding situations should be occupied first. These territories are the ones in which the male should become polygynous. Primary females should, therefore, settle earlier than monogamous females.

These predictions are tested to determine whether polygyny is costly to females, but compensated for, or not costly.

6.4. Methods

In line with other studies, first egg date (FED) was used as the best estimate of settlement date (e.g., Yasukawa and Searcy 1981; Leonard and Picman 1987; Lightbody and Weatherhead 1988; Leonard 1990). Females were often skulky and difficult to locate before nesting, so FED provided a good, measurable approximation to settlement time which was comparable between females.

Only first clutches were used in the analysis, firstly to prevent the re-use of individual females within the data sets for each year and secondly to avoid using FEDs for relay clutches which would obviously not truly represent the settlement date. Data from 1989 and 1990 were grouped.

Spacial dispersion of nests was examined by comparing the frequency distribution of nearest-nest distances for all first clutches against a Poisson (random) distribution calculated from equation 6.1 (from Brown and Downhower 1988).

$$\text{Poisson (random) distribution} = \sum_{n=0}^i (e^{-x})(x^n)/n! \quad (6.1)$$

where 'x' is the mean frequency per distance-group and 'i' is the number of individuals per distance-group.

Temporal dispersion of nests was examined using inter-nest intervals, calculated as the difference (days) between the FEDs of two females' first clutches. The inter-nest intervals of females nesting within territories were compared against a null model constructed from the inter-nest intervals of all pair-wise comparisons of FEDs from females nesting on different territories (Yasukawa and Searcy 1981).

Additionally the absolute extent of overlap (in days) was calculated for a 12 day nestling period for 15 pairs of females nesting on the same territories. Both first clutches and relays were used in this case.

Equation 6.2 was used (see appendix 2 for derivation) to determine the probability of two nests overlapping, in time, by chance alone, given that 'B' is the length of the population breeding season (the day the first egg was laid to the day the last nest fledged or was predated), and 'a' is the nestling period.

$$p(\text{overlap}) = \frac{(2a - 1)(B - a + 1) - (a^2 - a)}{(B - a + 1)^2} \quad (6.2)$$

In this case B = 92.5 days (mean of 1989 and 1990) and a = 12 days for the nestling period.

6.5. Results

6.5.1. Nest dispersion in space and time

Nearest nest distances for first clutches were distributed as shown in Fig. 6.3. There was a significant shift in the observed distribution towards aggregated nests (Kolmogorov-Smirnov $D_{\max} = 0.219$, $N = 47$, $p < 0.05$). Nests were therefore more clumped than expected by chance.

Inter-nest intervals (days) for pairs of females nesting within territories were not distributed significantly differently to those of pairs of females nesting on different territories (Kolmogorov-Smirnov $D_{\max} = 0.127$, $n = 510$, $m = 12$, $p > 0.1$; Fig. 6.4). Despite this there was very little overlap between females nesting within territories for the critical period when competition for resources, such as male parental care, might have occurred (the 12 day nestling period). Twelve pairs of within-territory females had temporally separate nestling periods and three others overlapped by one, six and seven days. The mean separation between the end of the first nestling period and the start of the second was 7.7 days (± 10.7 s.d., $n = 15$). The probability of finding two nests overlapping by chance during their nestling periods was $p = 0.262$. So for the 15 pairs of nests mentioned above, equation 6.2 predicts that 3.9 pairs would have overlapped by chance alone, which was not significantly different from the observed number of three ($\chi^2 = 0.156$, $df = 1$, $p > 0.5$).

6.5.2. Female settlement within male territories

There was no significant relationship between the order of settlement on territories by primary females and their corresponding secondary females ($r_s = 0.320$, $N = 13$, $p > 0.2$; Fig. 6.5).

There was no significant difference between the corrected first egg date (chapter 3) of the first settling female on territories where the male was either monogamous or bigamous (Mann-Whitney $z = 0.361$, $p > 0.7$; Fig. 6.6).

6.6. Discussion

6.6.1. Nest dispersion in space

Corn bunting nests were more aggregated than expected by a random distribution. This observation in itself does not provide strong evidence for a lack of female-female competition for resources because it is likely that females were aggregated in areas where there was suitable nesting habitat. Chapter 5 has shown that male territories were important to females for nesting habitat rather than for foraging habitat. In a study of corn buntings in Denmark, Møller (1983) found that male territories were under-dispersed, compared to a random Poisson distribution, and also concluded that this was due to aggregation of resources.

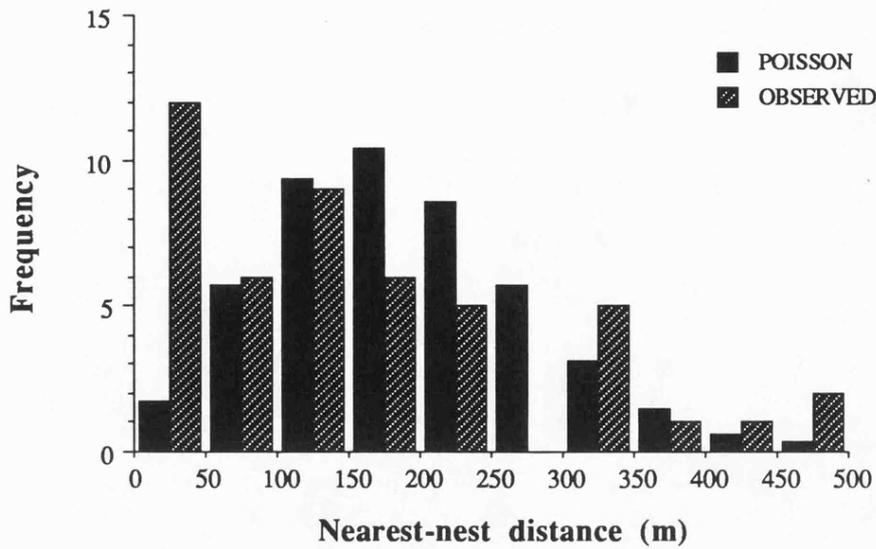


Fig. 6.3. Frequency distribution of nearest-neighbor distances (m) for first clutches, showing the observed distribution and a Poisson (random) distribution obtained using equation 6.1. The observed distribution was significantly different from the Poisson distribution (Kolmogorov-Smirnov $D_{max} = 0.219$, $N = 47$, $p < 0.05$). Nests were more aggregated than expected from a random distribution.

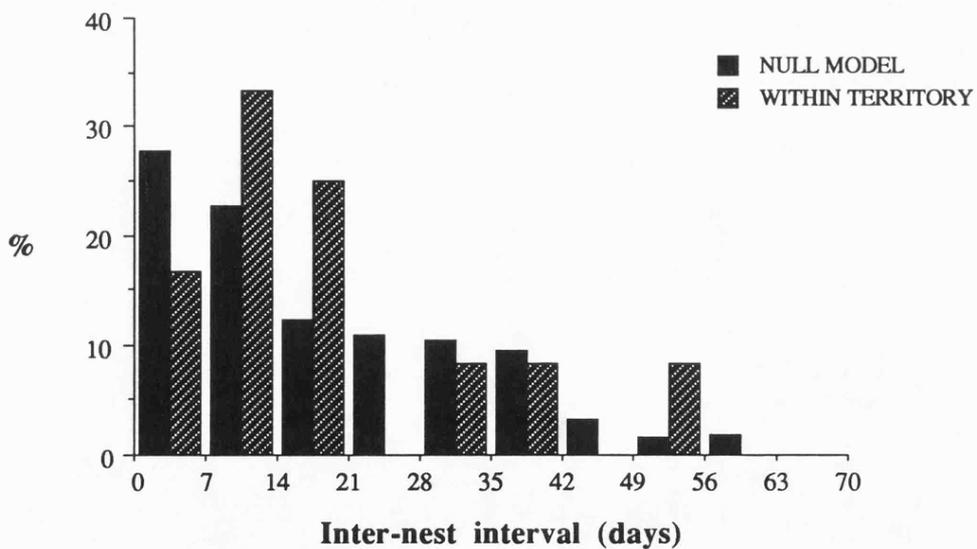


Fig. 6.4. Percentage frequency distribution of inter-neighbor intervals (days) between first egg dates of females within territories and on different territories (null model). There was no significant difference between the two distributions (Kolmogorov-Smirnov $D_{max} = 0.127$, $n = 510$, $m = 12$, $p > 0.1$).

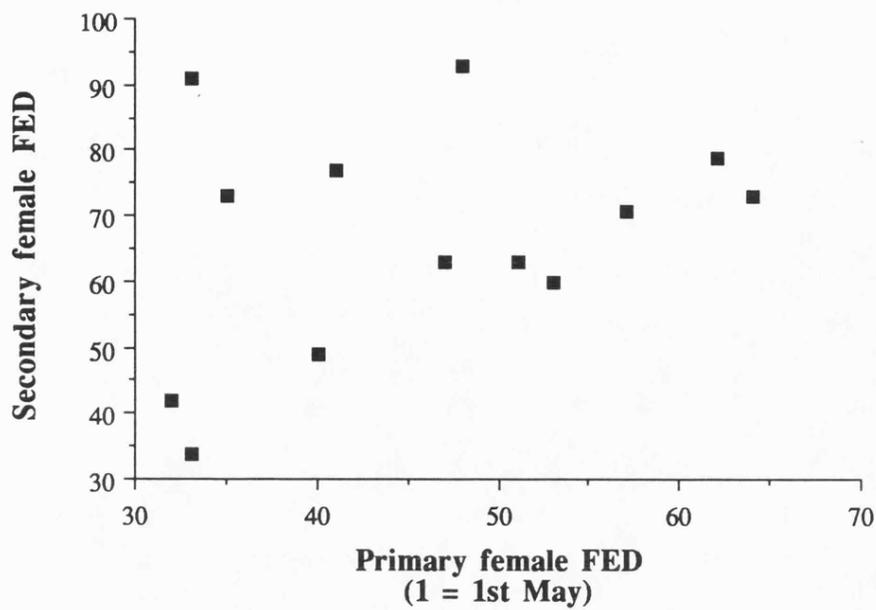


Fig. 6.5. Scatterplot of first egg dates (FED) for first clutches of primary and secondary females nesting on the same male territories. There was no significant relationship between the two variables ($r_s = 0.320$, $N = 13$, $p > 0.2$).

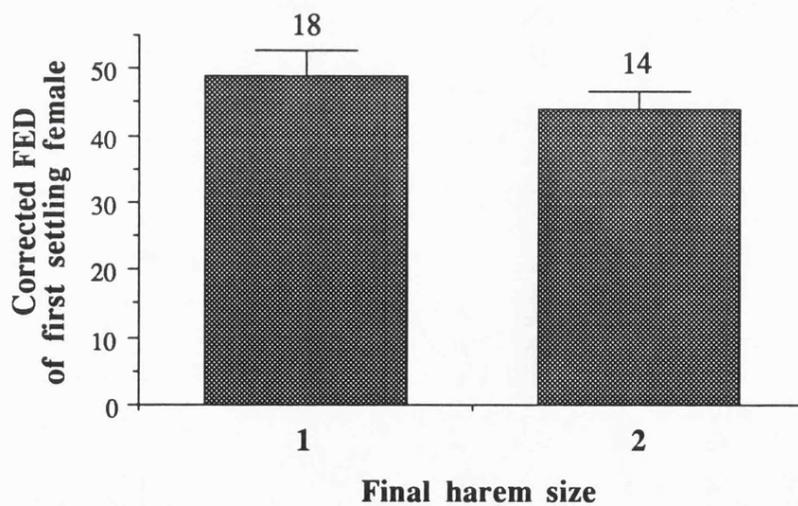


Fig. 6.6. Corrected first egg dates (1 = 1st May) for first settling females of bigamous males and monogamous females (mean \pm s.e., n). There was no significant difference between the groups (Mann-Whitney $z = 0.361$, $p > 0.7$).

Nest clumping may have been either beneficial, neutral or detrimental for the following reasons:-

1) Beneficial:- Females could benefit from group nest defence, as has been reported in bank swallows (Hoogland and Sherman 1976), Florida scrub jays (Wolfenden and Fitzpatrick 1984) and red-winged blackbirds (Picman *et al.* 1988), although there was no evidence for this in corn buntings (chapter 3). Other possible benefits could have included enhanced foraging ability due to following successfully foraging females (Ward and Zahavi 1973, but see also Mock *et al.* 1988).

2) Detrimental:- Grouped nesting may not be optimal but may be the best of a bad job brought about by the aggregation of nesting habitat. This does not seem to offer a reasonable explanation, however, because the closest nests are those of primary and secondary females nesting on the same territories, and the most isolated are nests of monogamous females. I have shown previously (chapter 3) that primary and secondary females have similar reproductive success and both are more successful than monogamous females, which indicates that there is no important cost to aggregated nesting.

3) Neutral:- There is no evidence to suggest that females benefit from nesting with an under-dispersed distribution and there is evidence against it being detrimental. The most likely explanation, especially in the light of other evidence below, is that the spacial dispersion of corn bunting nests was due to the aggregation of nesting habitat rather than the costs and benefits of grouped nesting.

6.6.2. Nesting dispersion in time

Yasukawa and Searcy (1981) found that in one population of red-winged blackbirds nests of females on the same territories were more asynchronous than nests on different territories and they attributed this to female-female competition for male parental care. Similarly, Leonard and Picman (1987) and Leonard (1990) showed that polygyny in marsh wrens was facilitated by asynchronous nesting of females within harems as this reduced the competition for resources at the critical nestling stage. Derrickson (1989) suggested that, in Northern mockingbirds, female-female aggression may reduce the possibility of a male becoming polygynous, but asynchrony or spacial distance between nesting females could reduce aggression and enable polygyny to occur.

In this study, nests of primary and secondary females within territories were not more or less synchronous than pairs of nests on different territories and although most pairs of within-territory nests were asynchronous (80.0%), they were not more asynchronous or synchronous than expected by chance. This suggests that females did not compete for resources, such as male parental care or nest sites, as they seem to in other polygynous species (Orians 1969; Altmann *et al.* 1977; Yasukawa and Searcy 1981; Leonard and Picman 1987; Lifjeld *et al.* 1987; Alatalo *et al.* 1988; Lifjeld and Slagsvold 1989;

Leonard 1990).

6.6.3. Female settlement within male territories

A prediction of compensation models of polygyny, such as the PTM, is that females should settle according to the quality of the breeding situation. When the polygyny threshold is reached, the next female to settle should choose the highest quality breeding situation, which would be the same as that chosen by the first (primary) female to settle. There should, therefore, be a correlation between the order in which primary females chose to settle and the order in which their corresponding secondary females chose to settle. Additionally, the males holding territories which were settled on latest should have been more likely to remain monogamous than males holding the earliest territories to be taken up, so that the first settling females on all territories should have been earliest on polygynous territories. No such relationships were found in this study, suggesting that females did not settle in relation to where other females were settling. This is further evidence that females were not competing for resources, as assumed by the PTM, and that the PTM was not an appropriate explanation for the maintenance of polygyny in the corn bunting.

The lack of any relationship between primary and secondary settling order on territories is consistent with the neutral mate choice hypothesis (Lightbody and Weatherhead 1988), as well as strong evidence against the PTM. Neutral mate choice could lead to polygyny if male territory size was directly related to the number of females settling, or if females settled randomly with respect to other females. If females were competing for resources other than male parental care, as appears to be the case in the yellow-headed blackbird (Lightbody and Weatherhead 1988), then females should be dispersed so as to avoid competition but might settle independently of male quality or resource holding potential. Female corn buntings do not settle with regard to other females, yet also seem to settle randomly with respect to males. As male territories do not vary for the resource which females choose (i.e. nesting sites, chapter 5), it is possible that one explanation for the maintenance of polygyny in corn buntings is chance. Sutherland (1985) showed that chance could explain variance in mating success equally as well as sexual selection theory. If a number of females settled randomly amongst an equal number of evenly sized territories, one would expect most territories to hold one female, some to hold two, some to hold none and a few to hold three: a binomial distribution. This is the pattern of female settlement observed in the corn bunting (chapter 2).

6.6.4. Rejection of cost models of polygyny in the corn bunting

Data presented here and in previous chapters suggest that female corn buntings do not suffer a net cost when pairing to a polygynous male. An alternative explanation would

have been that they were fully compensated for costs, as predicted by the PTM, but this hypothesis was not supported by data for settlement in either time or space.

Other reasons to reject cost models are discussed below.

6.6.4.1. Skewed sex ratio hypothesis

The sex ratio in this study was not skewed towards excess females. Ryves and Ryves (1934a, b) suggested that polygyny in corn buntings was caused by an excess of females but their suggested sex ratio of 2.3 females: 1 male was based on counts of nests per male rather than females, and as none of their birds were marked they could not know whether or not females were moving between males after failure, or were reneating. So, while they were obtaining an approximate harem size for their males they were not obtaining reliable data on sex ratios. If data from the present study were to be analysed in a similar way, using nests per territory rather than females, the apparent sex ratio would be 1.44 females: 1 male in 1989 and 1.83 females: 1 male in 1990. Other studies of corn buntings which used marked birds have found a 1:1 sex ratio (Gyllin 1965; Gliemann 1972; Hegelbach and Ziswiler 1979; Hegelbach 1984).

A vital prediction of the skewed sex ratio hypothesis for the maintenance of polygyny is that there should be no unpaired males in the breeding population, yet in this study 23.5% of males were unpaired over both study years (chapter 2).

6.6.4.2. Search cost hypothesis

The search cost hypothesis (Breihagen and Slagsvold 1988) does not explain the maintenance of polygyny in corn buntings because females nesting later in the season did not have a lower reproductive success than early nesting females (chapter 3), which suggests that the costs of not nesting as early as possible may be low. There is, however, the possibility that an early nesting female could successfully rear her first brood and still have time to raise a second, as a small proportion of females did indeed do (chapter 3). Although there is no evidence from this study to suggest that raising two broods per season was more costly to females than raising one, other studies have shown that parental care can be costly and may reduce the survival chances of the adults (e.g., Bryant 1979; Nur 1988; Ekman and Askenmo 1986; Gustafsson and Sutherland 1988; reviews in Clutton-Brock 1988 and Newton 1989). Therefore it is possible that there is a trade-off between life expectancy and double brooding which further reduces the costs of nesting later in the season. I suggest that searching for an unpaired male would not be as costly for a female corn bunting as it would for a pied flycatcher because pied flycatchers are migratory, have a short breeding season and females compete for the best nest holes (Breihagen and Slagsvold 1988).

The search cost hypothesis predicts that females should pair with unpaired males if they

have time to find them, yet in the present study polygynous and unpaired males often occupied adjacent territories, so it is unlikely that females were constrained by their ability to locate unpaired males, especially in such an open habitat as is found on the study site.

6.6.4.3. Deception hypothesis

The deception hypothesis (Alatalo *et al.* 1981, 1982, 1984a, 1991; Alatalo and Lundberg 1984; Catchpole *et al.* 1985) is very unlikely to account for the maintenance of polygyny in the corn bunting as they nested in an open, high visibility habitat (unlike great reed warblers [Catchpole *et al.* 1985]), polygynous males were never polyterritorial (unlike polygynous pied flycatchers [Alatalo *et al.* 1981, 1982, 1984a, 1991; Alatalo and Lundberg 1984; Lifjeld *et al.* 1987; Slagsvold *et al.* 1988; Lifjeld and Slagsvold 1989, 1990] and wood warblers [Temrin and Jakobsson 1988; Gyllensten *et al.* 1990]) and females were often seen together on the territory, but were very rarely aggressive towards one another. Ryves and Ryves (1934a) also comment on the fact that females on the same territories were rarely aggressive towards one another, despite the fact that encounters between them were common.

6.6.4.4. Sexual conflict hypothesis

The sexual conflict hypothesis (Davies 1989) suggests that polygyny has not arisen through female choice but through males taking advantage of the breeding situation at the expense of females. In other words, there is a conflict of interests between males and females, so that the best breeding options for each sex are not compatible. A prediction of this is that females should have lower reproductive success when they pair polygynously (the males' best option). This is not the case here, however, as monogamous females have a lower reproductive success than both primary and secondary females of polygynous males (chapter 3) and polygyny is apparently the best option for males as polygynous males have the highest annual reproductive success (chapter 2).

6.6.4.5. Maladapted female hypothesis

The maladapted female hypothesis was suggested by Searcy and Yasukawa (1989) as the 'last ditch' theory to explain the maintenance of polygyny when all else fails and seems an unlikely evolutionary possibility. If females were maladapted so that they chose low quality breeding situations despite the availability of better situations, they would not be in a stable evolutionary state. To put forward a neo-Darwinian argument (Dawkins 1976): if one female developed a mutant gene 'for' choosing the best available nest site, the gene would be selected for in favour of non-choosers, until an evolutionarily stable state was achieved in which all females had the gene and therefore selected the best nesting situation available to them.

6.7. Conclusion

Female corn buntings do not suffer costs in pairing polygynously, although there is no evidence to suggest that polygyny is directly beneficial to females either. Male corn buntings are probably polygynous by chance, because although females prefer to nest in uncultivated habitat, males do not show a large variance in the availability of such habitat within their territories, so females settling randomly with respect to males and other females nest on territories in a binomial fashion, such that some males are unpaired, most monogamous and some polygynous. Females are indeed distributed between males in a binomial distribution, rather than regularly (monogamy) or in a heavily skewed way (high polygyny, many males unpaired). This follows Sutherland (1985) in predicting that polygyny may arise by chance rather than choice.

If males did hold territories which were significantly variable in quality of resources needed by breeding females (e.g., nesting habitat), one should expect females to compete for the best territories and for those which held the best resources to be occupied first by females and be occupied by polygynous males. This was not the case here, however, as first settling females of polygynous males were no earlier settling than females of monogamous males. Also, if females settled according to territory quality, one should have expected secondary females to settle on territories in the same order as primary females, because both classes of female should have settled in the best breeding situation available at the time. This also was not the case here.

I suggest that males would maximize their chances of obtaining females if they defended as large an area of nesting habitat as possible, but they cannot monopolize more than their equal share because of intra-sexual competition for suitable territories. I cannot discount the possibility that some patches would be better than others, despite being equal in size, because of topographical features, such as dune ridges or small scale vegetation differences, which may, for example, provide extra shelter from harsh weather conditions or predators.

6.8. Summary

1) Existing models on polygyny in territorial birds are reviewed. Most effort has been put into testing individual models but a more productive approach would be to see which model best fits the species under study (Searcy and Yasukawa 1989), especially as some models are inappropriate for some species and therefore of little use in a test. It is important to test the assumptions of a model as well as its predictions.

2) Polygyny in corn buntings is investigated. One assumption of the polygyny threshold model is that females suffer costs to polygyny and compete for resources, such as male parental care, nest sites or food. Polygyny was not costly to female corn buntings

and females did not appear to compete for resources. Nests were under-dispersed in space, probably due to habitat aggregation, and were randomly dispersed in time within territories.

3) Primary and secondary females of polygynous males did not choose territories in the same order and the first settling females of polygynous males did not settle significantly earlier than monogamous females. This strongly suggests that males were not chosen because of the quality of their breeding situation but were chosen randomly. I suggest that male territories did not vary for area, or quality, of nesting habitat and so choosing randomly between males would not be detrimental to females.

4) A no-cost, no-benefit model with random female mate-choice is suggested as the best fit for a polygyny model to explain the maintenance of polygyny in the corn bunting.

Appendix 1. Scientific names of birds mentioned in the text.

fulmar	<i>Fulmarus glacialis</i>
oystercatcher	<i>Haematopus ostralegus</i>
moorhen	<i>Gallinula chloropus</i>
cuckoo	<i>Cuculus canorus</i>
European bee-eater	<i>Merops apiaster</i>
tree swallow	<i>Iridoprocne bicolor</i>
purple martin	<i>Progne subis</i>
bank swallow	<i>Riparia riparia</i>
barn swallow	<i>Hirundo rustica</i>
cliff swallow	<i>Petrochelidon pyrrhonota</i>
house martin	<i>Delichon urbica</i>
marsh wren	<i>Cistothorus palustris</i>
dunnock	<i>Prunella modularis</i>
pie'd flycatcher	<i>Ficedula hypoleuca</i>
collared flycatcher	<i>Ficedula albicollis</i>
great reed warbler	<i>Acrocephalus arundinaceus</i>
willow warbler	<i>Phylloscopus trochilus</i>
wood warbler	<i>Phylloscopus sibilatrix</i>
willow tit	<i>Parus montanus</i>
great tit	<i>Parus major</i>
blue tit	<i>Parus caeruleus</i>
starling	<i>Sturnus vulgaris</i>
house sparrow	<i>Passer domesticus</i>
yellow-headed blackbird	<i>Xanthocephalus xanthocephalus</i>
red-winged blackbird	<i>Agelaius phoeniceus</i>
bobolink	<i>Dolichonyx oryzivorous</i>
Eastern meadowlark	<i>Sturnella magna</i>
Northern mockingbird	<i>Mimus polyglottus</i>
Florida scrub jay	<i>Aphelocoma coerulescens</i>
zebra finch	<i>Taeniopygia guttata</i>
dickcissel	<i>Spiza americana</i>
indigo bunting	<i>Passerina cyanea</i>
reed bunting	<i>Emberiza schoeniclus</i>
corn bunting	<i>Miliaria calandra</i>

Appendix 2. Derivation of equation 6.2.

Equation 6.2 (reproduced below), was designed to predict the probabilities of two females overlapping for critical periods, such as the nestling period, when they may compete for similar resources, such as male parental care. For example, if the breeding season of an animal is short with respect to its breeding cycle, the chances of two females having overlapping breeding periods would be high, but if the breeding cycle is short in a long season, the probability of overlap would be low. Tests of nesting asynchrony must, therefore, take into account the actual probabilities of temporal overlap if the animals behave independently of one another.

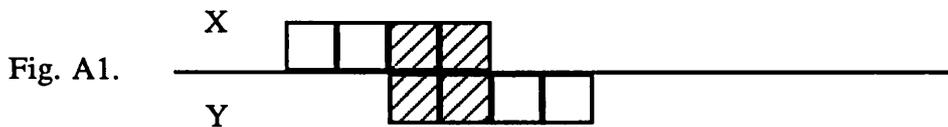
Equation 6.2 has two variables:-

'a' = the critical period

'B' = the length of the breeding season from the first egg to the last chick fledging

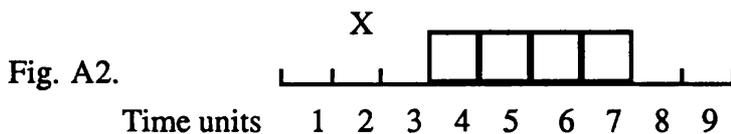
'a' and 'B' have the same units.

Two critical periods are considered to be overlapping if they overlap by one time unit or more. The possibilities of overlap are best described graphically:-



If animals X and Y each have critical periods of four units ($a = 4$), in Fig. A1 the periods are overlapping by two units and the possible ways in which they could overlap are $(2a - 1)$.

Fig. A2 shows, that for an animal having a critical period ($a = 4$) within a season ($B = 9$), there are $(B - a + 1)$ ways in which 'a' can fit into 'B' without overlapping the bounds of B.



So, animal X, with a critical period of $a = 4$, starts on unit four and ends on unit seven, but cannot start later than unit six or 'B' would have to be redefined. Each animal would have $(B - a + 1)$ possible positions along the time scale, so for two animals there would be

$(B - a + 1) \times (B - a + 1)$ possible combinations in which their critical periods could overlap.

Equation 6.1 is, therefore, the number of possibilities of overlap divided by the number of possible positions on the time line, which represents the breeding season for the two animals:-

$$p_{(\text{overlap})} = \frac{(2a - 1)(B - a + 1) - (a^2 - a)}{(B - a + 1)^2} \quad (6.2)$$

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