Sexual selection in the house sparrow, *Passer domesticus*

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by

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Abstract

Sexual selection in the house sparrow, *Passer domesticus*

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(1) This study investigated the maintenance of variation in the black throat patch or 'badge' of the male house sparrow. This sexually dimorphic trait is thought to be a sexually selected ornament, with previous workers providing evidence of a role in both mate choice of males by females and male-male competition. The study was conducted in 1995 and 1996 in a closed population of approximately 40 breeding pairs on Lundy Island, in the Bristol Channel, England.

(2) Genetic analysis of paternity using PCR-based microsatellite genotyping revealed a very low level of extra-pair paternity in both years and no intra-specific brood parasitism. Just three extra-pair chicks (1.0% offspring in 2.5% of broods) were discovered among 305 chicks in 112 broods. This low frequency of extra-pair paternity is significantly lower than the rates reported in three other populations of house sparrows and provides further evidence for a low level of extra-pair paternity occuring in isolated populations.

(3) The very low frequency of extra-pair paternity in this population allowed an examination of the costs and benefits that may be gained by a female exhibiting a preference for a large-badged male, unconfounded by the effects of extra-pair behaviour.

(4) The *direct benefits* models of sexual selection were tested by assessing male help in provisioning chicks at the nest. Counter to the predictions of these models, large-badged males contributed relatively fewer feeds than males with smaller badges. Similarly, large-badged males, and the females that chose them as mates, had lower annual fecundity and were predicted to recruit significantly less offspring into the breeding population.

5) A female preference might be driven by the *indirect benefits* of obtaining genes for either viability or attractiveness for the female's offspring. A cross-fostering experiment revealed that variation in badge size had a large environmental component with a strong correlation between offspring badge size and that of their foster father, with no discernible additive genetic variation. This mechanism for the determination of badge size cannot support a process of Fisherian 'runaway' selection and is consistent with those models which require a sexual ornament to be phenotypically plastic and therefore provide an honest signal.

6) Male fitness was investigated in relation to the expression of badge size. Males with large badges exhibited a higher level of overwinter survival, consistent with the predictions of a condition-dependent trait.

7) A model of lifetime fecundity suggested an intermediate optimum size for the badge. The results suggest that high fecundity is traded off against low survival, and vice-versa. This trade-off may maintain the observed variation of badge size and female preference.

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CHAPTER ONE

Sexual selection in the house sparrow (*Passer domesticus*)

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CHAPTER ONE

Sexual selection in the house sparrow (*Passer domesticus*)

"the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction"

Darwin (1871)

1.1 Introduction

1.1.1 Darwin's theory of sexual selection

The theory of sexual selection was born out of the paradoxical nature of certain traits which Darwin could not explain using his theory of natural selection (1859). The tail of the peacock (*Pavo cristatus*), or the antlers of red deer (*Cervus elaphus*) apparently do nothing to enhance the survival of an individual bearer. How can they have arisen in the first place, and how are such traits maintained? Darwin decided that such characters were concerned more with the production of progeny than survival of the individual. Sexually selected characters, or sexual traits, were the mediators of an unequal competition for mates and the production of offspring.

Two main forms of sexual selection were recognised; firstly, selection through direct competition between individuals of one sex, and secondly, selection for specific characteristics in one sex by the other choosy sex. Classic examples of each of these classes are, respectively, male-male competition in the red deer, in which males fight each other ritualistically and the winner monopolises a group of females and therefore gains paternity of the majority of the season's offspring (Clutton-Brock et al. 1988), and the train of the peacock, a sexual ornament which is attractive to females who mate preferentially with those males with the most elaborate displays, who, as a result, will be unequally represented in the next generation (Petrie & Williams 1993).

The demonstrated advantages to successful males make it easy to see how sexual selection could be responsible for the maintenance of traits that are apparently maladaptive under natural selection. The idea of sexual selection

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through male-male competition was quite easy to appreciate. The idea of females choosing males simply by the extent of a sexual ornament was less readily accepted. Why would females consistently choose a well ornamented male, and why should such traits become progressively more elaborate?

1.1.2 The Fisher process

The first attempt to model a solution to sexual selection through female choice was made by Fisher (1915; 1930). Fisher proposed a mechanism in which female choice would co-evolve alongside a male trait. The co-evolution of a female preference and a male sexual ornament would allow a male character to evolve directionally, under a runaway process, ultimately achieving an otherwise improbable size. Unilateral female choice and antagonistic natural selection (as in Darwin's original proposal), would generally not lead to such extravagant characters as some of those observed in nature. Fisher's idea was testable, and theoretically sound (O' Donald 1977; Halliday 1978; Lande 1981).

1.1.3 The handicap principle

One of the main criticisms of Fisher's model of runaway selection was that not all sexually selected ornaments have achieved the high degree of exaggeration that might be expected; many have apparently stabilised at a point below which we might expect natural selection to counterbalance them. For example, there are many sexually selected traits like the small forehead patch of the collared flycatcher (Gustaffson et al. 1995), which is very subtle and realistically can not be under any degree of direct natural selection. Outrageous sexual characters like the tail of the peacock are relatively uncommon.

In his book *The Genetical Theory of Natural Selection* Fisher (1930) hinted at 'good genes' mechanisms of sexual selection, however, his idea was largely ignored until Williams (1966) suggested that female mate preferences might evolve as a method of choosing the males with the most viable set of genes. The idea was formalised by Zahavi as the 'handicap principle' with his model of sexual selection based on the handicapping influence of sexually selected traits (Zahavi 1975). If a male could survive the handicap of bearing a large ornament then it would prove its phenotypic and genotypic fitness to females. An initial problem with this model was that it assumed no link between the trait and the genotype of the bearer, therefore every male will get a random

ornament and while highly ornamented males that survive will on average be more viable, all males with small ornaments will also presumably survive (Maynard Smith 1976). This complaint was addressed with the conditional handicap model (Zahavi 1977), in which the secondary sexual character is expressed relative to the quality of an individual. Under this model, different levels of ornament impose different costs on high and low-quality individuals, such that, a high quality male will pay less for a large ornament in terms of a handicap than a low quality male.

Another type of handicap is the revealing handicap. Hamilton & Zuk (1982) suggested that male sexual characters may be particularly sensitive to parasite infections and hence reveal male resistance to parasites.

In most of the handicap models it is assumed that the handicap and the trait will have a degree of heritability. For this reason, the handicap models are generally grouped as the 'good genes' hypotheses although, strictly, the Fisher process is also driven by females seeking 'good genes'. The benefits to females of mate choice in a handicap system are for her offspring (the genes they inherit), not herself, therefore they are generally termed the *indirect benefits* models.

1.1.4 Direct benefits

Due primarily to the constraints of egg-laying, the majority of bird species form monogamous pair bonds, at least throughout a reproductive cycle, with males providing a varying degree of parental care (Lack 1954). Monogamy puts several constraints on sexual selection and these have been recognised by the direct benefits models which typically apply to monogamous (and polygynous) systems.

The direct benefit models all predict a tangible gain to the female from her choice of mate. Such benefits, which may include access to male-held resources and male help, will generally lead to increased female fecundity. The 'sexy son' hypothesis, proposed by Weatherhead & Robertson (1979), was based on the observation that in red-winged blackbirds (*Agelaius phoeniceus*) some females pair with males that are already mated and therefore receive less parental care from those males. As a result, they will rear fewer offspring and, therefore, it might be assumed that their fecundity is lower. It is argued, however, that although they produce fewer offspring, the males may inherit their father's sexiness and therefore increase the fitness of the mother, albeit

in the next generation. The 'sexy son' hypothesis contains elements of both the indirect and direct benefits models, but as it was originally proposed as a direct fecundity benefit to females then it is generally categorised with the other direct benefits.

A more obvious direct benefit model is the good parent process. Female choice for those males with the best resources or parenting ability will pay obvious rewards. Heywood (1989) and Hoelzer (1989) both suggested that parental qualities of males may be more important to females than the indirect genetic qualities to be gained for their offspring. This good parenting hypothesis can only apply in monogamous systems and the benefits to females may be through nest sites, defence from predation or harassment from other males, fertility assurance, help with feeding chicks, and good resources such as territories (reviewed in Andersson 1994). The benefits to females may be realised immediately through higher breeding success or perhaps might be more subtle and realised through higher survival of the female and hence greater lifetime reproductive success (Stearns 1989). The specific predictions of the models of Heywood (1989) and Hoelzer (1989) are that a male trait will predict reliably to a female the extent of the benefit she can expect to gain, and that there is no need for the traits to have a genetic basis. The relationship observed between song quality and territory quality is a good example of how such a mechanism might work (Alatalo et al 1990). Male sexual ornaments based on carotenoid pigments may also be honest signals of the quality of males and their territories. Birds are unable to metabolise carotenoid pigments and, therefore, the quality of plumage traits that utilise them is dependent upon the quality of the environment and foraging ability of the individual expressing them; the red plumage of the house finch is a sexually selected trait which clearly operates in this manner (Hill 1990; 1991).

1.2 Empirically testing the models of sexual selection

During his life, one of Darwin's biggest problems was the testing of his theories of speciation. Since that time there have been many attempts to demonstrate examples of natural selection occuring in the wild, these were given a critical review by Endler (1986). Of these studies there are perhaps only a few which remain as classic, unambiguous examples of natural selection occuring. For example, there is the demonstration of the adaptiveness of the melanic form of the peppered moth, *Biston betularia* to industrial

environments in Britain (Bishop et al. 1978); adaptiveness of different colour patterns to predation pressure in different streams in Trinidadian guppies *Poecilia reticulata* (Endler 1980); and natural selection on several morphological characters by a severe drought in one of Darwin's finches, the medium ground finch *Geospiza fortis* (Grant 1986).

Generally, the time scale under which natural selection operates prevents a thorough experimental study. It is hoped that sexual selection will offer a much better chance to explore the mechanisms of selection and speciation. Sexual selection has several benefits over natural selection as a process for study. Firstly the traits which are the focus of sexual selection are by their nature conspicuous, and external and therefore often open to manipulation. Additionally, whilst natural selection may work on an organism in a myriad of different ways, concurrently, sexual selection tends to be more focused, and operates regularly on just one trait. For example, although many sexually selected species of bird have many plumage characters for example wing bars, eye stripes, chest patches, it is often found that only one or two of these are highly variable and used in sexual selection (Andersson 1994). This will reduce the number of confounding influences which potentially disrupt empirical tests of natural selection.

Throughout this century there has been a gradual expansion of the theoretical basis of the mechanisms of sexual selection, and by the end of the 1980's all the currently acknowledged mechanistic models had been formulated. Coincident to this, the field of molecular genetics had developed to a point which permitted a more rigorous testing of sexual selection. For example, to test sexual selection it was necessary to compare the reproductive success of individuals within a population. Although this had been attempted previously by simply counting copulations, or young in a nest, it was imperative that genetic tests were applied to accurately determine genetic input into the next generation. The inevitable fusion of molecular genetics and behavioural ecology has led to a thorough testing of the fully developed theory and a great progression in our understanding of sexual selection.

1.2.1 The significance of monogamy

Of all the currently known mating systems in the world, perhaps one of the most pertinent to ourselves is that of monogamy (given that it predominates in our own culture). Due to the constraints of egg laying it also occurs in over 90% of bird species (Lack 1968; Gowaty 1996). Initially, it would seem that

monogamy is the system least likely to yield great insight into sexual selection, with little chance of a reproductive skew within one population (assuming that the operational sex ratio is equal, all individuals will get a chance to reproduce). Trivers (1972) was the first to suggest that perhaps individuals of both sexes would be best served by pursuing alternative mating strategies. Even within the confines of monogamy it was suggested that through such a strategy some individuals could increase their reproductive success at the expense of others hence, causing a skew in reproductive success. The strategies which Trivers proposed were extra-pair paternity (EPP), and intra-specific brood parasitism (IBP) in birds.

In birds, IBP is the laying, by a female, of an egg in the nest of another con-specific. Potentially it could be a useful strategy for a female to adopt in an effort to increase overall reproductive output and does indeed occur across a wide range of avian families. However, the observed very low levels (under 2%) in a wide variety of species (reviewed in Yamauchi 1993) suggests that in most species mechanisms have evolved to counter the threat of being parasitised and the behaviour is not widely significant with respect to reproductive success.

The other alternative mating strategy suggested by Trivers, EPP is very common, being observed more frequently than not throughout socially monogamous bird species (Birkhead & Møller 1992), and occurring at a wide variety of levels (currently between 0 and 55%, Owens & Hartley 1998). EPP is the occurrence, within a brood of offspring, of individuals who are fathered by a male who is not the pair male. Although it can occur through forced copulation of females by males (McKinney et al. 1983), it is now mostly considered to occur through the seeking of extra-pair copulations (EPCs) by females (Birkhead & Moller 1992).

The benefits to a male of gaining EPP are obvious; EPP will increase his reproductive success without incurring any costs of parental care. The costs to a male of indulging in EPCs are not quite so clear, although he may incur costs from his pair female, such as losing his female or paternity of his own clutch to another male (Birkhead & Møller 1992), or risk contracting a sexually transmitted disease (Sheldon 1993). Females potentially share most of the same predicted costs as males from participating in EPCs, but potentially suffer an extra cost through a reduction in parental care from the male. There are two reasons for this discrepancy; firstly, females will have made a higher investment than the male in the eggs, in terms of both time and resources.

Secondly, whereas females will be assured of the maternity of the eggs they lay, males cannot be as sure of their paternity. If a male 'suspects' that he has lost paternity then the most adaptive response will be to reduce parental care (Dixon et al. 1994) and attempt to increase his reproductive success elsewhere. The cost to a female of having her infidelity discovered is therefore expected to be high, particularly as it is assumed that reproductive success in monogamous species benefits from having both a male and female in attendance at the nest.

A female is unable to increase her reproductive output substantially through EPCs, however, some of the predicted benefits could potentially lead to a slightly higher reproductive success. These benefits may be direct, for example assurance against infertility (Lifjeld 1994; Sheldon 1994) or access to resources (Gray 1997) or may be indirect and benefit the female via the fitness of her offspring (Williams 1966). The main potential indirect benefits are a higher genetic diversity of the brood (Westneat et al. 1990), or most notably the gaining of good genes for the offspring either for viability (Hamilton & Zuk 1982) or for the expression of a sexual trait (Fisher 1930).

1.2.2 The use of EPP to test theories of sexual selection

If we assume that successful fertilisation following forced copulation of females is unlikely to occur (a reasonable assumption in most passerines due to the lack of an intromittant organ and, therefore, the relative ease with which females can mechanically prevent successful ejaculation into the cloaca [Birkhead & Møller 1992]), then those males successful in gaining EPP will have been selected by females for whatever benefits they can offer. There is a small problem herein; to date, no one has reliably measured the relationship between success at gaining EPCs and gaining EPP. It is possible that only a subset of those males indulging in EPCs are actually successful in gaining EPP through the mechanisms of sperm competition and cryptic female choice (reviewed in Eberhard 1997). Whilst this is a gap in knowledge, it is hereafter assumed that those males successful in acquiring EPP are representative of those participating in EPCs. It could also be argued that only males successful at gaining EPP will actually count anyway as that is what will effect sexual selection.

In a monogamous system, the most attractive males potentially could increase their reproductive success dramatically simply by producing sperm and indulging in EPCs, leading to a great skew in the reproductive success of males

and hence increased sexual selection. In a socially monogamous system, it is likely that the reproductive skew will be greater through EPP than through within-pair reproductive success. Studying extra-pair mate choice, as opposed to pair mate choice, will give us a direct insight into this reproductive skew. Secondly, for a female extra-pair mate choice does not operate under the same constraints as pair mate choice. In a truly monogamous system each male will only pair with one female. Assuming that pairing will only start at a given date, for example the start of the breeding season, an unpaired female will only ever have the choice of the unpaired males i.e. those that are left. The same female, choosing a male with which to indulge in an EPC will find that she has a much greater choice of males willing to mate with her. The study of extra-pair mate choice should therefore give greater insight into the benefits of female choice.

Although less constrained, it is unrealistic to believe that extra-pair mate choice is totally unconstrained, as it is expected that not all males will indulge in EPCs freely. All males will have a limited amount of sperm which will need to be invested in the most adaptive manner (Birkhead et al. 1994), and the risk of contracting a sexually transmitted disease may increase male choosiness regarding which females, and how many, they are willing to copulate with. There are also conflicting reproductive interests which may prevent many males from participating in EPCs at a given time; e.g. mate guarding (reviewed in Birkhead & Møller 1992) and investment in offspring in their own nest (Gowaty 1996). All of these things may limit the availability of males willing to indulge in EPCs; however, we can still assume that generally, for all females, extra-pair mate choice will be less constrained than the choice of a mate.

1.2.3 The empirical test of sexual selection

To study sexual selection via female choice, the fundamental question that needs to be addressed is:

What does a female gain from her choice of mate?

This question can be tackled via her choice of a pair male and even more interestingly through her choice of extra-pair mates.

As already outlined, the potential benefits are direct or indirect. The direct ones are perhaps easier to address and generally concern the female's choice of

partner. These benefits can be studied in a wide variety of species with no particular constraints on the type of population used. The study of indirect genetic benefits, which are of a more subtle nature, requires a particular approach, population and species. The main indirect benefit that may be sought by females are good genes for either viability or the expression of a sexual trait. To study either of these, it is important to be able to follow the survival and reproductive success of individual offspring throughout their lives and to monitor the production of sexual traits, and the success of individual genetic lineages. Furthermore, to disassociate environmental and genetic influences on both viability and trait expression, it is necessary to cross-foster offspring (Gustaffson 1986). It is also important to be able to assign all offspring to their fathers, whether these are extra-pair or within pair. A comparison of the sexual traits and general viability between extra-pair and their within-pair siblings will provide a thorough empirical test of the good genes hypothesis.

The success of such a study requires a closed or inclusive population which will prevent dispersal of individuals and allow an accurate measurement of individual life histories. Additionally, a species is required that is open to the manipulation of nestlings and which is relatively easy to work with. Finally, of course, the species must have a trait which is assumed to be sexually selected.

1.3 The study species and population

1.3.1 The house sparrow (*Passer domesticus*)

The house sparrow is a small passerine belonging to the family Passeridae. At a weight of approximately 28 g and 14-15 cm in length, it is the typical 'small brown bird'. The sexes are dimorphic, the male being very slightly bigger (<3%) than the female (Johnston 1981)(Figure 1.1). There is a great degree of dimorphism in plumage, with the female being dull brown and lacking any conspicuous markings. The male has rich chestnut and brown contour feathers with a prominent black throat patch (or 'badge' : Dawkins & Krebs 1978) and eye stripe, a slate grey mantle to the head, white eye spot behind the eye and a white wing bar (Figures 1.2, 1.3 and 1.4). Both sexes can vocalise but the female is restricted to a very simple 'cheep'. The male, in addition to this 'cheep', is capable of slightly more elaborate song consisting of 'chirrup, chirrup' and a very simple trill. This song is used in courtship behaviour by the males to attract a mate to the nest site and also simultaneously with a

simple 'dance' which serves to highlight the throat patch (Summers-Smith 1963).

House sparrows are highly gregarious and prefer the company of others all year round. They do not establish territories and the only area which they will defend to the exclusion of other sparrows is a very small area around their nest (< 0.25 metre). Under natural conditions they prefer to nest in loose colonies and are capable of nesting at very high densities, with adjacent pairs often nesting within half a metre of each other. They are one of the most widespread species in the world (partly due to introductions by man and due to their commensal nature), and are capable of breeding under many circumstances. Here I will restrict discussion to their normal breeding behaviour at the chosen study site. House sparrows are very sedentary and will generally remain for their whole life in one location. Any dispersal seems to be restricted to juveniles and is quite limited (Fleischer 1984); in Britain, the British Trust for Ornithology (BTO) ringing scheme reports it as exceptional for a house sparrow to be recovered more than a few kilometres from a previous encounter (BTO pers. comm.).

House sparrows are capable of breeding in the year following the one in which they fledged. Due to the sedentary nature of the house sparrow and the close flocking behaviour of populations between autumn and spring it is likely that pairing of males and females probably takes place at any time during the six months before the start of the breeding season. Pairs generally remain faithful to one another across several breeding seasons (Veiga 1996). This mate fidelity is of course hampered by the high rate of annual mortality of adults, in many cases only one member of a pair will survive to the following breeding season.

The breeding season begins properly when males select nest sites and begin to defend these from other males and start to display to females. The male will also begin to line the nest cavity with straw. Once they have paired, they complete the nest together and begin to copulate frequently from up to 5 days before the first egg is laid, the fertile period of the female begins three days before the first egg is laid (Birkhead et al. 1994). Once laying begins the female will lay one egg each day soon after dawn until the clutch is complete. The average size of clutch in the study population is 4.2 eggs, S. D. = 0.963, n = 67.

Incubation begins on the day the last egg is laid. Only female house sparrows have a brood patch (a bare patch of skin heavily supplied with blood vessels) because they alone have to incubate the eggs. The males can assist to varying

Figure 1.1 The male and female house sparrow
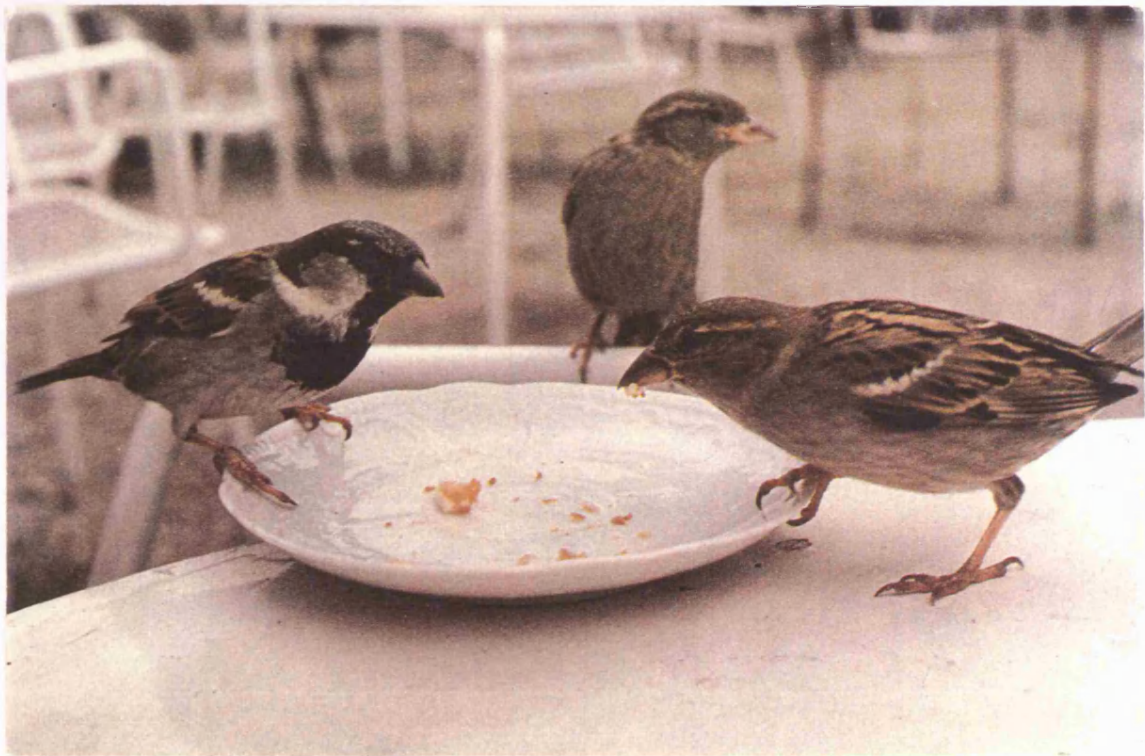
Figure 1.2 The male house sparrow (with colour rings)

Figure 1.3 The black throat patch of the male

Figure 1.4 The sparrow's view of a male (feathers raised in alarm)

degrees by guarding the nest when the female is absent and maintaining the warmth of the eggs. Incubation lasts for approximately 12 days and then the chicks should all hatch within 24 hours. There is often some incomplete hatching failure; wherein just some of the eggs within a clutch fail. In the study population 13% of eggs failed to hatch in clutches in which at least some hatched. There were a few cases in which there was total failure. Following hatching, the chicks are then reared in the nest for approximately 15 days until they fledge. Again during this period there is usually some failure from predation, or starvation of the weaker members of the brood. In the study population there were no nest predators and all chick mortality was caused by partial brood starvation, leading to a mean of 2.0 fledglings (S. D. = 1.22, n = 64) per clutch. Once the chicks have fledged they require feeding by either parent (the relative effort by each sex is unknown though both males and females have been recorded feeding juveniles 15 days after fledging pers. obs.), out of the nest for about another 10-20 days before they become totally independent (Summers-Smith 1963).

Being multi-brooded, house sparrows are capable of several breeding cycles during one breeding season. In 1995 all the pairs in the study population had two broods, and in 1996 they nearly all managed to have three broods. The breeding season at the study site begins in late April and continues through to August.

The house sparrow is a good study species for several reasons. Firstly, it is extremely common on a worldwide scale and lives very closely associated with man. It is generally considered to be a pest which means that there are no conservation implications of working with it. Also they occur in highly accessible locations and will be tolerant of a reasonable level of human disturbance. Secondly, it is a cavity nester and will take readily to artificial nest boxes, so allowing easy access to eggs and chicks. Thirdly, there has been a large amount of work conducted on many aspects of the species' biology, which is a great asset to both the study and interpretation of results. Finally, being very common, well known, and so clearly dimorphic it has already been a focus for some of the early work in the field of sexual selection (e.g. Møller 1987a, b; Maynard Smith & Harper 1988). Despite no absolute proof, previous work on other populations of house sparrows by several other groups led us to assume that the black throat patch was a sexually selected trait. Although initially it seemed that this sexual selection was largely through male-male competition (Maynard Smith & Harper 1988; Møller 1987), work by Møller (1988) indicated that females did exhibit a preference for large-badged males.

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1.3.2 The Lundy population

This study was carried out on the population of house sparrows on Lundy Island. Lundy is situated in the Bristol Channel, approximately 20 km off the north coast of Devon, England (51"11' N, 4"40' W) (Figure 1.6). The island is approximately three kilometres long by one kilometre wide and the habitat is generally unsuitable for the house sparrow. The study population is therefore restricted to an area of about one square kilometre at the south-eastern corner of the island around the village (see Figures 1.5 and 1.7). This village consists of approximately 20 buildings which are used as holiday and residential accommodation throughout the year, there is also a public house (very important for the sparrows), restaurant, and shop. The remainder of the village is taken up by farm buildings. The current farm is probably operating at its smallest level this century and consists of about twenty chickens, several pigs, and 600 domestic sheep, the latter being grazed largely outside of the sparrows range. The existence of the farm is probably essential to the sparrow population, particularly over winter, as they scavenge on the feed of the chickens and pigs and rely heavily on the bedding and food of sheep housed indoors.

Historically sparrows have been on the island probably as long as man (thousands rather than hundreds of years). This century, they were certainly present until the 1940's (Lack 1942), when they were purposefully eradicated because of the pressure they exerted on grain supplies (Lundy Field Society Journals 1956-present day). The presence of a bird observatory on the island during the subsequent period and the records provided by the Lundy Field Society are invaluable in helping to build a picture of the history of the current population. Apart from occasional individuals which turned up on the island at a rate of approximately three every four years and did not stay, the first birds became resident and bred in 1972. Since that time, house sparrows have bred annually on Lundy, and the population has grown through natural regeneration, presumably supplemented by a continued low level of immigration. The population size appears to have been relatively stable at around 50 breeding pairs.

Figure 1.5(a) Map of the range of the study population including the location of the artificial nestboxes
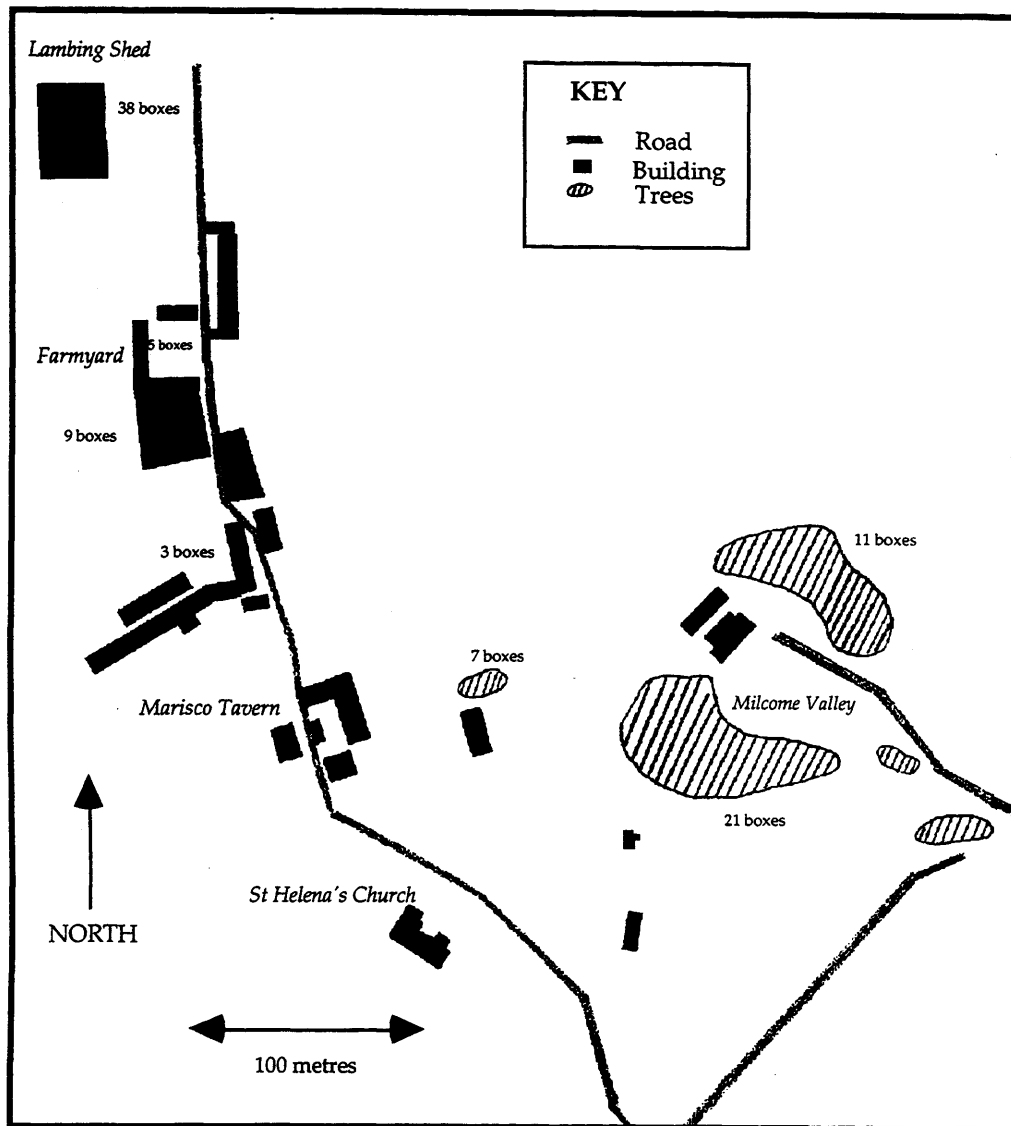
(b) Lundy in the Bristol Channel   **(C)** The study area on Lundy
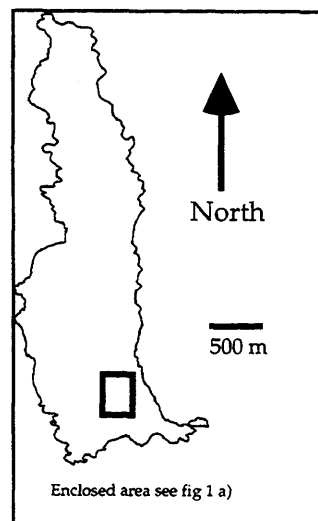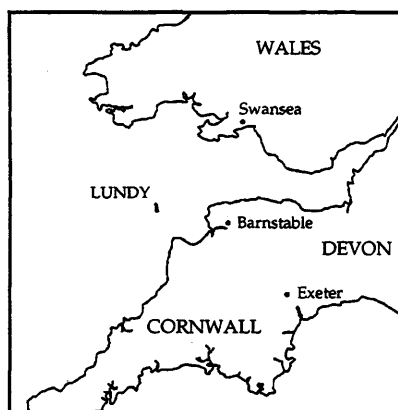
Figure 1.6 Lundy Island

Figure 1.7 Lundy village

During the time (1950's to the 1970's) that sparrows were absent from the island and the bird observatory was operating, house sparrows were recorded as occasional vagrants. They were found to turn up at a very low rate (less than two individuals every two to three years [Lundy Field Society Journals 1956-present day]). There is no reason to believe that this level of immigration has increased, particularly as the population on the mainland has declined in recent years (Glue 1994). Also, despite many years ringing on Lundy, no bird has ever been relocated on the mainland. We can assume, therefore, that individuals not found to be present on the island during a survey have indeed died.

The study of this population was initiated by I. P. F. Owens who in 1990 erected nest boxes throughout the breeding area, and discouraged or prevented the sparrows from nesting in their traditional nest sites (holes under roofs and in stone walls). Efforts were also made to catch and ring all individuals with uniquely numbered BTO aluminium rings and a unique combination of plastic colour rings. Following on from the effort by Ian Owens to mark birds and monitor the population throughout 1990-1994 the work presented in this thesis was conducted between January 1995 and December 1997. At the outset of this project a culture of using nest boxes was well established among the sparrows on the island and following more intensive work, this culminated in 1997 in 100% of breeding attempts being made in artificial nest boxes. Similarly, in 1995 it was estimated that approximately 30% of individuals on the island were ringed with a metal (BTO) ring and approximately 10% also had colour rings, but by the winter of 1996 100% of birds on the island were ringed with metal and colour rings. A small population in which all birds are visually identifiable through the use of colour rings, and which is restricted in its movements, allows very accurate estimates of the survival of individuals and good opportunities for the retrapping of individuals. As far as possible, the characteristics of a population ideally suited for the study of the indirect benefits of sexual selection were largely met although the sample size is quite small on an annual basis and therefore not ideal.

1.4 The thesis

1.4.1 Aims of the thesis

This thesis describes a study of the maintenance of variation in the expression of a sexual ornament, the badge of the male house sparrow. This issue is primarily tackled from the point of view of the female house sparrow. If females do prefer males with large badges, as has been suggested (Møller 1988, 1989), then what are the potential benefits that can be gained from this preference? Using predictions made by the currently accepted models of sexual selection for a male ornament (Andersson 1994), the indirect (Fisher 1930; Williams 1966; Zahavi 1975, 1977; Hamilton & Zuk 1982; Grafen 1990a, b), and direct benefits (Heywood 1989; Hoelzer 1989) of female choice will be empirically tested.

The specific aims of this study were as follows:

(1) To design and evaluate primers to be used for PCR (polymerase chain reaction) amplification of microsatellite loci in the genome of the house sparrow to be used for genotyping the population and paternity scoring.

(2) To determine the level of EPP within the study population through the sampling of whole families in the field and the use of the genotyping system out lined above.

(3) To determine direct benefits females will gain from males by quantifying chick-feeding behaviour of males at the nest and also by monitoring realised reproductive success of all pairs in the population.

(4) To determine the variation of male badge size throughout the population and also that of other morphological traits in both males and females.

(5) To determine indirect benefits to females of mate choice through a cross-fostering study which assessed the contribution of additive genetic variation to badge size.

(6) To determine life-history costs to both males and females with respect to reproductive effort and badge size in the male.

1.4.2 Chapter summaries

This thesis is composed of eight chapters, each (except the introduction and discussion) in the basic format of a scientific paper. In each chapter the predictions from the literature are introduced and the results are discussed and set within the context of the other empirical work.

Chapter 1 introduces the theoretical background to the study, the study species and study site.

Chapter 2 describes the genetic methodology used to conduct the paternity analysis and reports the genetic mating system on the island.

Chapter 3 describes the measurement of the male contribution to chick-feeding and investigates the relationship between variation in badge size and this direct benefit.

Chapter 4 investigates the relationship between variation in badge size and the variation in reproductive success of pairs in the population.

Chapter 5 investigates the mortality cost of reproductive effort on adult house sparrows as demonstrated through a brood size manipulation.

Chapter 6 tests the generally accepted idea that sexual selection is counterbalanced by natural selection with showy males suffering higher levels of predation.

Chapter 7 describes the results of the cross-fostering study which determines the contribution to badge size variation of additive genetic variation and also environmental components.

Chapter 8 summarises all the empirical evidence and uses a simple model to illustrate the mechanisms underlying the maintenance of variation in the size of the badge of the male house sparrow.

CHAPTER TWO

Genetic monogamy in an island population of a socially monogamous bird, the house sparrow

2.1 Abstract

2.2 Introduction

2.3 Methods
      2.3.1 Study population
      2.3.2 Molecular methods for investigating paternity

2.4 Results and discussion
      2.4.1 Why is the extra-pair paternity rate so low on Lundy?

CHAPTER TWO

Genetic monogamy in an island population of a socially monogamous bird, the house sparrow

"The incredible English sparrow is the best illustration of
furor amatorius. The male suffers from satyriasis,
the female from nymphomania"

Bent (1958)

2.1 Abstract

Previous studies have shown the level of extra-pair paternity in the house sparrow to be consistent at around 15%. This paper reports a thorough study of the genetic breeding system of a small isolated population of house sparrows in which the rate of extra-pair paternity is significantly different from other estimates in this species and approaches, almost uniquely for a dimorphic passerine bird, genetic monogamy. Two new microsatellite markers were isolated and characterised and used alongside two previously published house sparrow microsatellite markers to test for the occurence of extra-pair paternity in 305 offspring from 112 broods in 1995 and 1996. The overall level of extra-pair paternity was found to be just under 1% affecting 2.5% of all broods.

2.2 Introduction

House sparrows are socially monogamous, with the pairbond lasting at least the course of one breeding effort, and often through subsequent nesting attempts within or even between seasons (eg, Veiga 1992, 1996). The successful rearing of offspring is enhanced by the attendence of both parents during the whole rearing cycle, and although incubation is carried out by the female, provisioning of the young is shared equally (Summers-Smith 1963).

Because of the advantages of biparental care in many species of passerine bird, alternative mating strategies are one of the few ways in which males and females can significantly augment their annual reproductive success (Trivers 1972; McKinney et al 1984). For instance, through indulging in extra-pair copulations males have the chance to increase the total number of young fathered in a breeding season and females may be able to improve the genetic quality or diversity of their offspring (Williams 1966; Brown 1997; Birkhead & Møller 1992), assure fertility (Wetton & Parkin 1991, c.f. Lifjeld 1994), or gain direct benefits in terms of access to resources (e.g. Gray 1997). Indeed, such alternative reproductive strategies appear common among birds, with Owens & Hartley (1998) reporting that extra-pair fertilizations have been found in 69% of the 35 putatively monogamous species in which molecular techniques have been used to assign paternity. In previous studies of house sparrow populations the level of extra-pair fertilizations has been found to be: 14% (Wetton et al. 1995), 12% (Kimball 1995); and 11% (I. Stewart *pers. comm.*).

The overall aim of this study was to investigate sexual selection in the house sparrow, with a particular focus on female choice of male phenotypic traits. However, to address this issue it is first essential to assess the genetic mating system of this putatively monogamous population. For instance, do all females indulge in extra-pair behaviour? If not, which males lose paternity within their broods? Which males gain extra-pair paternity? Similarly, is extra-pair paternity randomly distributed among clutches, or is it associated with a particular male trait such as large badge size (see Wetton et al. 1995; Møller 1988, 1990)?

The value of assessing the genetic mating system of a further population of house sparrows is that differences between populations, but within a species, in the rate of extra-pair paternity will help to address the fundamental question: what are the mechanisms that drive extra-pair behaviour?

2.3 Methods

2.3.1 Study population

The study population was on Lundy Island (51.11 N, 4.40 W), an island of approximately 3 km^2 situated 20 km off the south west coast of Devon, England, and has been studied by us since 1990. Historically, there was a population of house sparrows on Lundy from at least the last century until the mid 1940's, when sparrows on the island were eradicated due to perceived

pressure on grain production after the Second World War. The current population established itself following breeding by an immigrant pair in 1972 and was subsequently supplemented by a low level of natural immigration. Because between 1944-78 there was a bird observatory on the island, and there were no resident house sparrows, the natural rate of immigration to the island could be estimated and was found to average approximately three birds every four years (Journals of the Lundy Field Society 1960-95). Also, as house sparrow numbers on the mainland have been declining since 1972 (Glue 1994), it is unlikely that this rate of immigration has increased. The Lundy Island house sparrows constitute a largely closed population from an ecological, though not genetic viewpoint.

During 1990-97 the size of the study population remained stable at around 40 breeding pairs. Nestboxes were introduced in 1990 and are now used by all pairs. The population occupies an area of 1 km^2 centred around a village farm at the south-eastern corner of the island. The sparrows nest at relatively high density (up to 25 boxes per hectare) in two main breeding areas: one around the village farm buildings (45 boxes) and one in neighbouring trees (37 boxes). In any one year there were several unused nestboxes but over the full period of study since 1990 all were used at least once. Nestbox density ranged from 'solitary' boxes (nearest box approx ten metres) to 'colonial' boxes (nearest box within one metre) (see Figure 1.5a).

House sparrows do not hold territories and the whole population mixes freely at communal feeding, bathing, and roosting sites. All individuals in the population were uniquely colour-banded for individual recognition in the field, including a numbered British Trust for Ornithology (BTO) metal ring for identification in the hand. Nestboxes were watched during the feeding of chicks to allocate parents to broods. To this end, approximately two hours was spent watching each box to observe a total of about ten visits by each parent. Only two adults were ever seen feeding each brood. The work reported in this paper was carried out between May and August in 1995 and 1996.

2.3.2 Molecular methods for investigating paternity

To facilitate the potentially complex task of assigning paternity to chicks, a microsatellite-based genotyping system was employed (Hanotte et al. 1994; Primmer et al. 1995).

Blood (ca. 30 µl) was taken from the brachial vein of adult birds and stored in 100% ethanol; chicks were sampled at 2 and again at 11 days old. DNA was extracted from whole blood using a simple chelex resin-based extraction method which makes small amounts of DNA available in solution (Walsh et al. 1991). Four hypervariable microsatellite loci were used: two previously published (*Pdo*µ3 and *Pdo*µ4); (Neumann et al. 1996) and two (*Pdo*µ5 and *Pdo*µ6) from dinucleotide and tetranucleotide microsatellite libraries isolated in Leicester. A ligation of pBluescript II plasmid to house sparrow DNA enriched for di- and tetranucleotide microsatellites was kindly supplied by D. Dawson. This ligation mix was created using a method based on Armour et al. (1994) with modifications as described in Gibbs et al. (1998). Briefly it can be summarised as follows:

i) Genomic house sparrow DNA from an individual female (HS33576) was extracted, purified, and digested with *Mbo*I.

ii) Fragments were then ligated to *Sau*3AI linkers. These linkers were made by annealing equimolar amounts of Sau-L-A (5' - GCGGTACCCGGGAAGCTTGG - 3') and 5' phosphorylated Sau-L-B (5' - GATCCCAAGCTTCCCGGGTACCGC - 3') as described by Royle et al. (1992).

iii) DNA was size selected for 300-600 base fragments by electrophoretic separation in agarose.

iv) DNA was separately hybridized overnight in phosphate/SDS buffer with the enrichment filters CA and TTTC at 65°c and 60°c, respectively. Target DNA consisting of poly-(TTTC) was prepared for this filter as in Armour (1994).

v) The filters were stripped to recover the DNA which was PCR-amplified using the linker sequence to produce the complementary strand and increase the number of copies available to be cloned into the vector.

vi) The linkers were removed using *Mbo*I and the DNA (now double-stranded) was ligated into *Bam*HI digested pBluescript II vector.

This ligation mix was then transformed into recombinant bacterial colonies which were grown on media containing Xgal and IPTG and screened. Colonies containing an insert appear white whereas colonies containing no insert appear blue. White colonies were picked and grown onto filters which were

then screened using radioactive hybridisation with either synthetic oligonucleotide probes of GT/CA (Pharmacia) or TTTC/GAAA probes PCR-generated from 24-mer tetra-repeat oligonucleotides (Armour et al. 1994) labelled with ^{32}P. Those colonies which hybridised with the probes were grown up to high yield and DNA was extracted using the Promega Wizard miniprep kit. This DNA was then sequenced using an ABI 373A automatic sequencer.

Table 2. 1 Summary of effort from the production of ligated colonies to the design of primer sets.

Outcome	CA.GA	TTTC.GAAA
Total number of colonies grown	2000	1000
Number of white colonies probed	480	192
Number of autoradiograph positives produced	65	5
Number of positives sequenced	31	5
Duplicated inserts	1	0
Less than 15 dinucleotide repeats	16*	-
Less than 10 tetranucleotide repeats	-	1
Repeat too close to vector (GATC)	2	-
Inserts containing no repeats	0	0
Inserts containing more than one repeat	1	0
More than 15 dinucleotide repeats	5	-
More than 10 tetranucleotide repeats	-	2
Large number of repeats and primers designable	6	2
Primer sets designed and tested	2	2
Succesful amplification of polymorphic microsatellites	1	1

* seven of these were complex micros with a long repeat broken up with other bases, i.e. 6, 5, 12

Of those sequences which contained short tandem repeats thought to be of reasonable size (15 repeats for di- and 10 repeats for tetranucleotides), four were chosen for the development of primer sets. Primers were designed using the primer design software PRIMER (Lincoln 1991). The primer sets were then tested on a panel of 20 different house sparrows which included some family groups. They were checked for heterozygosity and that the microsatellites were inherited in a Mendelian fashion. Conditions for the PCR reaction were also optimised at this stage to give clean products. Of the four primer pairs only two gave clean variable products; one of these was used for this study along with two previously published primer pairs from Neumann et al. (1996) (see Table 2.2). All the microsatellite loci used were originally isolated in the house sparrow.

Table 2.2 Characterisation of four house sparrow microsatellite loci based on 48 adults from the Lundy population. Ppat is probability of false paternal exclusion, calculated from observed allele frequencies (see Jamieson 1965). The size given is that of the original sequenced clone. Characterisation of Pdoμ5 based on 26 adults from the lundy population.

Locus	Repeat motif	Primer sequences 5'-3'	size (bases)	No. of alleles	Observed heterozygosity	P_{pat}
Pdoμ3 †	(CCAT)	F: CTGTTCATTAACTCACAGGT	140	10	0.78	0.283
		R: AGTGAAACTTTAATCAGTTG				
Pdoμ4 †	(GAAAGAGA)	F: CGATAAGCTTGGATCAGGACTAC	375	16	0.90	0.159
		R: CTTGGGAAGAGAATGAGTCAGGA				
Pdoμ5*	(CA)	F: GATGTTGCAGTGACCTCTCTTG	230	10	0.92	n/a
		R: GCTGTGTTAATGCTATGAAAATGG				
Pdoμ6	(GAAA)	F: CTGATCATGTGTAGATGTAAGACTGC	330	15	0.79	0.187
		R: CAGATCCTTAAGCAGGAAGTTAGG				
					combined	0.0084

† As previously published by Neumann et al (1996); Genbank accession numbers X93505-X93506. Loci Pdoμ5 and Pdoμ6 were submitted to Genbank (accession numbers Y15125-Y15126).

For each locus, the polymerase chain reaction (PCR) was carried out in a Perkin Elmer DNA thermal cycler using the following PCR profile: an initial hot start for 2 min at 94°C, followed by 35 cycles of 20 s at 94°C, 30 s at annealing temp, 60 s at 72°C. Annealing temperatures were 54°C for Pdoμ3 and Pdoμ4 and 59°C for Pdoμ5 and Pdoμ6. Each 15-μl mix included 0.1 unit of Taq polymerase (Pharmacia), 10 μl Jeffreys' buffer (final volume: 20 mM (NH4)2SO4, 75 mM Tris-HCl pH 8.8, 0.15 mg/ml DNAse free BSA, 10 mM ß-mercaptoethanol, 2.5 mM MgCl2; Jeffreys et al. 1988), 0.8 μM of each primer and approximately 10 ng genomic DNA. Products were resolved on a 6% denaturing polyacrylamide gel alongside a 50-base-pair ladder (Gibco BRL) and visualised by silver staining (Bassam et al. 1991).

Allele sizes were size scored by comparison with the size marker (50-bp ladder). Although this did not allow for precise size determination, it was possible to group PCR products into discrete allele classes which may have contained products of slightly different sizes ± two base pairs. Twenty individuals were run and scored on three different gels to assess the accuracy of this approach. The assigned alleles were consistently scored as being distinct from one another.

Using a panel of 48 unrelated adults, allele frequences were scored for each of the loci (26 adults in the case of Pdoμ5)(Figure 2.2). The probability of false paternal inclusion (P_{pat}) was calculated for each locus following Jamieson

(1965)(Table 2.2). The cumulative probability of false paternal exclusion when using just three (*Pdo*μ3, *Pdo*μ4 and *Pdo*μ6) of the microsatellite primers in this population was found to be 0.0084 and deemed sufficient to score paternity, therefore locus *Pdo*μ5 was not used.

Figure 2.2 Allele frequencies at three microsatellite loci (N = 48).

Pdoμ3

Pdoμ4

Pdoμ6
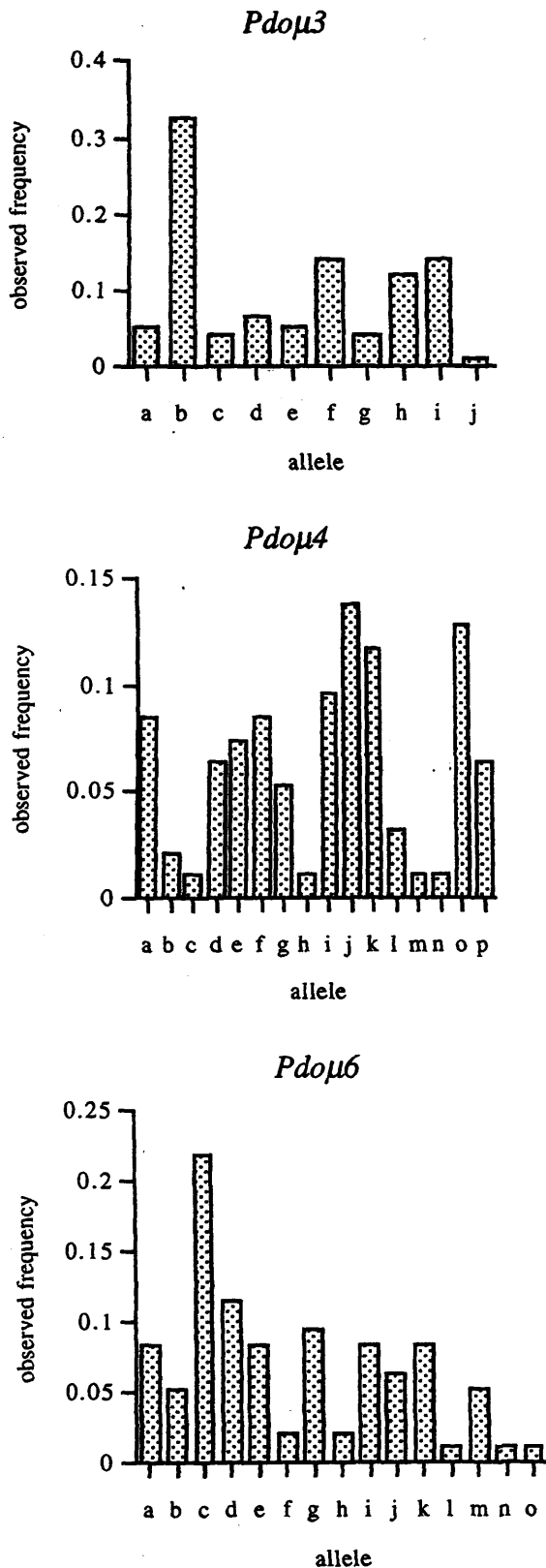
2.4 Results and discussion

A total of 112 broods were sampled from 71 different pairs. From a total of 305 chicks, 18 mismatched with their putative parents at at least one locus. However of these 18, 15 mismatched at just one of the three loci. 13 of these were found to mismatch at locus $Pdo\mu4$, a level consistent with the reported mutation rate of this loci (0.022, 95% c.i. 0.068-0.004 (Neumann & Wetton 1996)). Just 3 individuals of 305 mismatched with their putative parents at more than one loci of these three, closer examination revealed that they all shared common alleles with their putative mother but not the putative father. Offspring were determined to be the result of extra-pair copulations when two or more alleles mismatched with those of the attendant maleHence they were determined to be the products of extra-pair copulations as opposed to the result of intra-specific brood parasitism. With just three extra-pair offspring out of 305, the level of extra-pair paternity in this population is just less than 1% (see Table 2.3) (offspring were determined to be extra-pair when two or more alleles mismatched with those of the attendant male).

Table 2.3 Frequency of extra-pair paternity in the two years of study. EPY is extra-pair young, EPP is extra-pair paternity.

	no. pairs	no. broods	total chicks	no. EPY	EPP % young	EPP % broods
1995	30	38	107	2	1.9	5.2
1996	41	74	198	1	0.5	1.4

The observed level of extra-pair paternity is exceptionally low when compared with the estimates for 17 other species of putatively monogamous passerines, in which the mean rate of extra-pair paternity was 20.9% (95% confidence interval = 17.6-24.2%; Owens & Hartley 1998). More interestingly, however, the level of extra-pair paternity was significantly different from the rates found in other studies of the same species (13.6% offspring, Nottingham, UK, Wetton & Parkin 1991; 12.7%, New Mexico, USA, R. Kimble *pers. comm.*; 10.5%, Kentucky, USA, Stewart & Westneat *pers. comm.*). This is unusual because the limited data for those species in which two, or more, populations have been analysed show that the rate of extra-pair paternity observed in one population is significantly correlated with that observed in the other population (see Figure 2.3, also Owens & Hartley 1998 for full data). In other words, the rate of extra-pair paternity appears to be a species characteristic. Further duplication between different populations within a single species will

perhaps reveal other within-species differences which may shed light on the factors driving and maintaining alternative mating strategies.

Figure 2.3 Relationship between the rates of extra-pair fertilisation found in different populations of the same species (adapted from Owens & Hartley 1998). Studies were randomly assigned to population #1 and #2. Unfilled circle refers to previous studies of population *Passer domesticus*, filled circles refer to studies of species other than *Passer domesticu* s(1. *Ficedula hypoleuca*; 2, *Sturnus vulgarus*; 3. *Parus caeruleus*; 4, *Delichon urbica*; 5, *Progne subis*; 6, *Hirundo rustica*; 7, *Tachycineta bicolor*; 8, *Agelaius phoeniceus*). *r* refers to linear correlation coefficient, *n* refers to sample size, and *p* refers to the associated two-tail probability (regression performed on data set with *Passer domesticus* excluded). See Owens & Hartley (1998) for original references. note this relationship remains significant when point 7 is removed.

Extra-bond paternity in population #1
(% offspring)
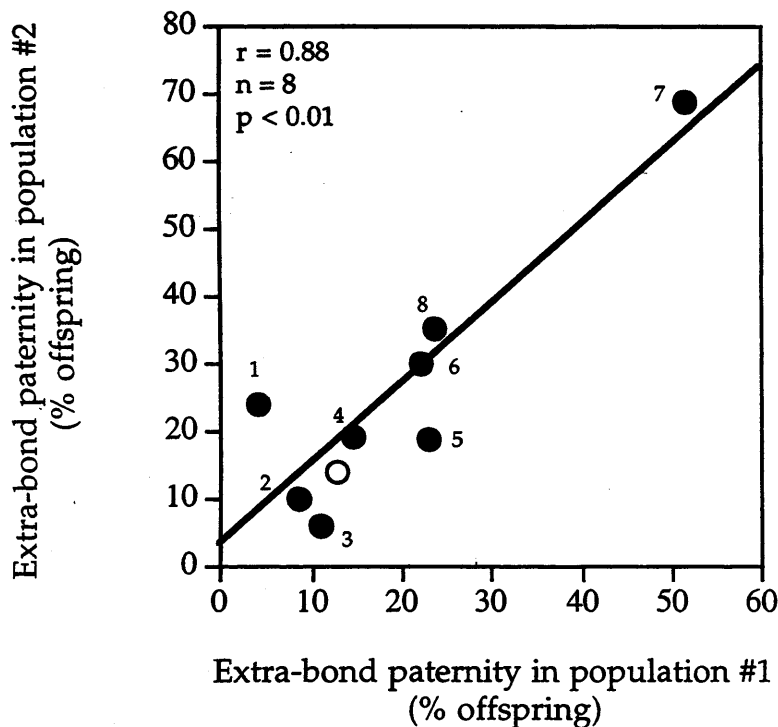
2.4.1 Why is the extra-pair paternity rate so low for the Lundy population of sparrows?

The most obvious potential explanation for the difference in the rate of extra-pair paternity is variation in breeding density - high density has been predicted previously to lead to high rates of extra-pair paternity (Westneat 1997). However, the spatial breeding distribution of the Lundy population is comparable to that of the other populations (see Table 2.4). Indeed, in some areas the Lundy population breeds at a higher density than the mean for the other populations. It seems unlikely, therefore, that the low level of EPP was caused by simple spatial effects influencing the proximate availability of alternative mating opportunities.

Table 2.4 Frequency of EPP in different populations of the house sparrow.

Population	Level of EPP	Ave. nearest neighbour (m)	Reference
Nottingham, UK	14.0%	5	Wetton &Parkin 1991
Lundy Island	1.0%	7	This thesis
Helgeland, Norway (archipelago)	4.7%	5	I. Stewart pers com
Kentucky, USA	10.5%	5	I. Stewart and D. Westneat pers com
Albuquerque, USA	12.7%	Unknown	Kimball 1995

The finding of a low level of extra-pair paternity in the Lundy Island population may also be relevant to current ideas concerning the ultimate role of genetic diversity in determining mating systems (Petrie & Lipsitch 1994; Petrie & Kempenaers 1998). Genetic variation is expected to be reduced in island populations due to a combination of founder effects, inbreeding, genetic drift, and low rates of dispersal (Wright 1931; Jaenike 1973). Indeed, a recent comparative study across many taxa, including birds, found that island populations did show significantly lower levels of genetic variation compared with mainland populations (Frankham 1997).

While the general consequences of reduced genotypic variance are largely unknown, there is evidence for reduced fitness, e.g. in an isolated population of the song sparrow (Keller et al. 1994). Regardless of such fitness reductions, it has been predicted that the level of genetic variance will affect the frequency of extra-pair paternity (Petrie & Lipsitch 1994). Specifically, in a population of low genetic diversity in which all males are essentially very similar, the benefits to females of seeking extra-pair copulations are decreased with the costs remaining the same (only with a good genes model of sexual selection). Hence, the costs to females of extra-pair behaviour in terms of reduced parental care (Dixon et al. 1994) and increased exposure to pathogens (Hamilton 1990) may outweigh the potential benefits of good genes (Williams 1966; Kempenaers et al. 1992) and genetic diversity (Brown 1997), and we might therefore expect the rate of extra-pair paternity to decrease. However, in order to test whether genetic and phenotypic variation does indeed drive the prevalance of extra-pair paternity, we will need to conduct a comparative study of different populations within a species or manipulate individual populations between breeding seasons.

CHAPTER THREE

The good parenting hypothesis: are sexy males better parents?

3.1 Abstract

3.2 Introduction

3.3 Materials and methods

       3.3.1 Study population

       3.3.2 Measurements

       3.3.3 Analysis

3.4 Results

       3.4.1 Male

       3.4.2 Female

       3.4.3 Pair provisioning rate

       3.4.4 Relative male provisioning rate

3.5 Discussion

CHAPTER THREE

The good parenting hypothesis: are sexy males better parents?

3.1 Abstract

The cause of persistent variation in male sexual ornaments has been explained by several models citing female choice of particular male phenotypes for the gain of direct benefits. Direct benefits are predicted to increase her own fitness through the acquisition of tangible resources from the male. Here we set out to test the 'direct benefits' model through the hypothesis that those males with the largest sexual ornaments will provide higher levels of parental care to the brood than their smaller badged counterparts. In the study species, the house sparrow *Passer domesticus*, chick-feeding at the nest was taken to be the most significant benefit a female could potentially gain from her partner. We found that large-badged males provided significantly less care to offspring than their small-badged counterparts, the opposite of the prediction of the 'direct benefits' model. Whilst these results are in general agreement with the differential allocation model we propose a new more parsimonious model, the 'lazy male' hypothesis.

3.2 Introduction

Empirical work suggests that the black throat patch , or 'badge' of the male house sparrow is a sexually selected trait with large badged males being preferred by females both as social partners and sexual mates (Møller 1988, 1989, 1992; Maynard-Smith & Harper 1988; but see Kimball 1996). If we assume this suggestion to be true, the obvious question is, why do females prefer to pair with large badged males? Theories on the adaptive basis of female choice can be divided into two non mutually-exclusive sets; those based on 'genetic effects' and those based on 'direct benefits (reviewed in Kirkpatrick & Ryan 1991; Andersson 1994). Specifically, females may choose a large badged male as a partner to gain good genes (eg. Fisher 1930; Pomiankowski 1987; Zahavi 1975,1977), or else to gain increased reproductive success through acquisition

of resources; nest site, protection, and parental care (eg Hoelzer 1989; Heywood 1989).

Perhaps because of their greater theoretical difficulty, the genetic-benefit ideas have traditionally received the greater attention (see Andersson 1994). For example, the good genes hypothesis predicts that females choose male partners based on the expression of a secondary sexual trait correlated with heritable genetic quality, such as the ability to resist parasites (Hamilton & Zuk 1982). Or alternatively, the Fisherian 'runaway' hypothesis predicts that, where male secondary sexual characters are heritable, females that choose sexy males will produce sexy sons (Fisher 1930; Lande 1980; Pomiankowski et al 1991).

The best known example of the direct benefits theories is the 'good parent hypothesis' which predicts that there is a positive correlation between the size of secondary sexual characters and provisioning effort (Hoelzer 1989). Hence, under this scenario, the secondary sexual character advertises a non-heritable component of parental quality. The aim of this study was to test the relevance of this hypothesis to the maintenance of female choice and male badges in the house sparrow. Here, the good parenting hypothesis predicts that male badge size in house sparrows should be positively correlated with male provisioning rate (eg. Møller 1988, 1989,1990).

3.3 Materials and methods

3.3.1 Study Population

This study was conducted between January 1995 and August 1997 on Lundy Island, situated in the Bristol Channel 20 Km off the south west coast of England. The study population of house sparrows *Passer domesticus* consists of approximately 40 breeding pairs nesting exclusively in nest boxes. All adults on the island have been caught using mist nets, walk-in, and nestbox traps and are rung with metal BTO rings and colour-banded with individual combinations for identification in the field.

The population lives within an area of approximately 1 km² in a village farm. One hundred nestboxes have been sited throughout this area but are concentrated in two main places, within a small wooded area, and around a barn. The whole population ranges over the entire area and uses communal feeding sites and traditional roosts.

The majority of social bonds are monogamous but there was a low level of polygyny within the population (7.5% of males have more than one social partner). However, all pairs resulting from polygynous bonds have been excluded from this analysis due to the constraints that polygyny imposes on provisioning of both male and females (Veiga 1990, 1992). Additionally, genetic work has shown that nearly all females are genetically faithful to their partner, with a very low level of extra-pair paternity in the population (less than 1 % of 305 chicks) (Chapter Two).

This population of house sparrows is ideal to study the relationship between sexual selection and parental care for a number of reasons. First, the readiness of the sparrows to use nestboxes means that all pairs are easy to observe and nest sites are broadly similar across pairs. Second, males do not defend territories and, therefore, all birds potentially have access to the same resources. Third, because there are no nest predators present on the island, nestling provisioning is the single most important feature of parenting ability. Finally, the very low level of extra-pair paternity is important because male parental care has been demonstrated experimentally to reflect a male's certainty of paternity in both polygynous and socially monogamous avian species (Davies et al 1992, Dixon et al 1994, Møller 1988, Whittingham et al. 1993, Yezerinac et al. 1996, and Wagner et al. 1996). The results of this study will, however, be unconfounded by the effects of alternative mating strategies.

3.3.2 Measurements

The black throat patch of male house sparrows is produced once a year during the moult in late summer. When first produced, the feathers which make up the badge are mainly black but have a pale buff tip. Initially, these buff tips conceal the blacker regions of the feathers and the full extent of the throat patch is concealed throughout the winter and into the spring. As the tips wear off, the badge becomes more visible but its visible size will always be dependent upon the extent to which the buff tips have worn away (Møller 1987; Veiga 1996). Hence, in order to obtain a repeatable measure of 'badge size' the length of the badge from the base of the birds bill to the posterior limit of the badge was measured at the base of the feathers using calipers. During the breeding season this 'hidden' area is highly correlated with the area of the visible badge ($r^2 = 0.47$, $n = 47$, $p < 0.001$). Also, this measurement is highly repeatable throughout the whole year, not just when the buff tips have worn off ($r = 0.755$, $F_{12,13} = 7.778$, $p < 0.001$; calculated after Falconer (1960)). Badge

length, rather than badge area, was used as an index of badge area because the former was found to be more repeatable.

Individuals were measured following Svensson (1984) including wing length (maximum chord,flattened) and weight to the nearest 0.25g. Tarsus measurements were made with vernier calipers from the posterior notch at the inter-tarsal joint to the front of the tarsal bone with toes bent down. The residuals from a linear regression between body mass and tarsus length were used as a body condition index (BCI).

Once breeding had commenced, nestboxes were checked every second day to ascertain hatching date. On hatching (day one), chicks were individually marked by nail clipping and were weighed. Thereafter they were checked again on day four, then eight, and ringed on day eleven. From these few visits it was possible to determine how many chicks were present at any given time and therefore deduce the timing of any partial brood mortality.

The rate of chick feeding by both the male and female was estimated by watching nests throughout the nestling period, with both sexes scored simultaneously. Focal nests were watched repeatedly for periods of 20 minutes between day two and fledging (usually about day 16). Watches were conducted using a telescope (20x) from a distance of not less than ten metres by a hidden observer and between the hours 05.00-09.00 BST to minimise confounding temporal effects. Active nests were randomly assigned an observation time on each given day. All data presented here were collected between day four and eight of the chick rearing period, before this time females tend to spend a lot of time brooding the chicks. All data presented here was gathered in 1996 and thefore will not be confounded by the brood manipulations which occured in 1995 and are discussed in later chapters.

3.3.3 Analysis

Unless otherwise stated, measurements of chick feeding rate are presented as visits to the nest per chick, per hour. This measure will remove the effect of different chick numbers in focal nests (range 1-6, mean 2.52).
Data was tested for normality using Lilliefors test (Wilkinson 1992). Residuals of regressions were also checked for normality , in both cases a probability of $\leq$ 0.05 was taken to indicate biological significance. Linear regressions were carried out using the SYSTAT package.

3.4 Results

There was substantial variation in provisioning effort among males within the population (Figure 3.1). The mean rate of male provisioning effort was 2.295 ± 0.78 SD. visits per hour, per chick. This variation was maintained when we looked at male provisioning effort as a proportion of total pair provisioning effort. Here, the mean proportion of feeds that were provided by the male was 0.393 ± 0.065 SD. The mean rate of female provisioning effort was 3.516 ± 0.99 SD. visits per hour, per chick. Again there was substantial variation between different females (Figure 3.2).

Figure 3.1a) Variation among males in absolute rate of feeds per chick, per twenty minute period. Error bars indicate ± standard error. Variation between different males is greater than that within individuals, (ANOVA $F_{34,329} = 3.208$ $p < 0.001$).
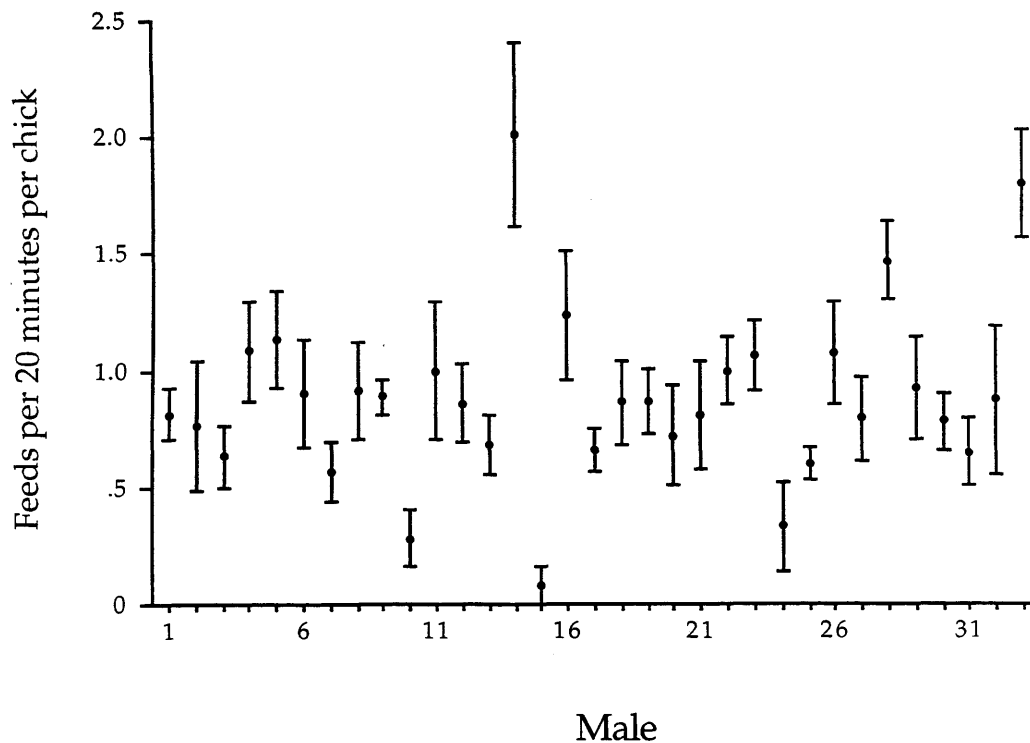
Male

Figure 3.1 b) Variation among males in the proportion of total pair feeds delivered. Error bars indicate ± standard error. Variation between different males is greater than that within individuals, (ANOVA $F_{34,328}$ = 3.319 p < 0.001). The female proportion of total feeds is obviously the inverse of the male in each case.
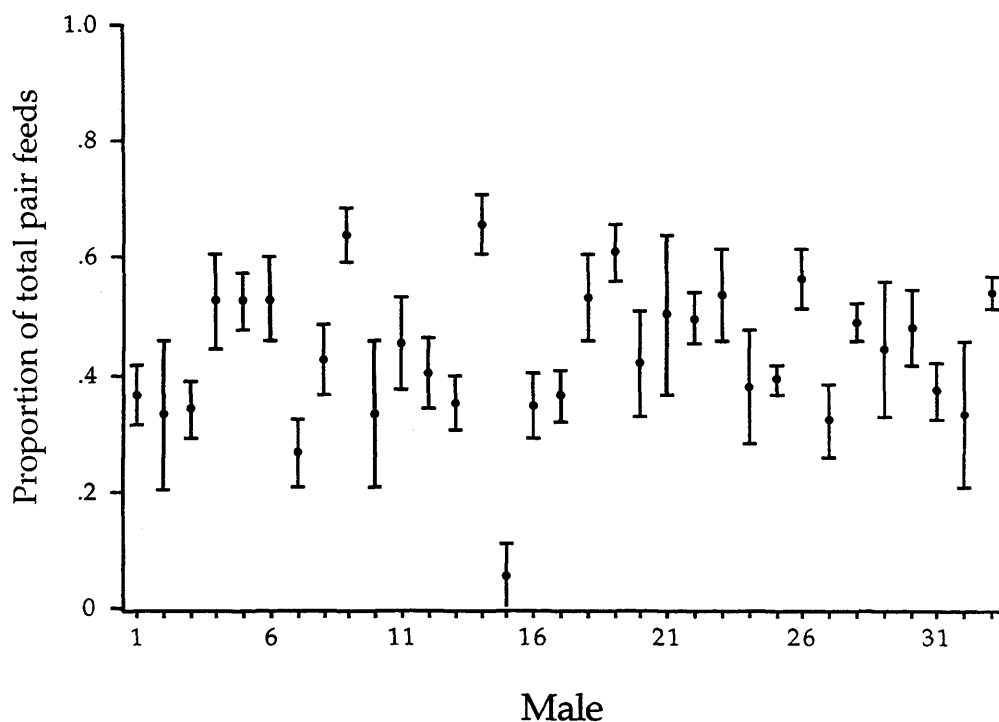
Male

Figure 3.2 Variation among females in rate of feeds per chick, per twenty minute period. Error bars indicate ± standard error. Variation between different females is greater than that within individuals, (ANOVA $F_{34,329}$ = 2.303 p < 0.001).

Female
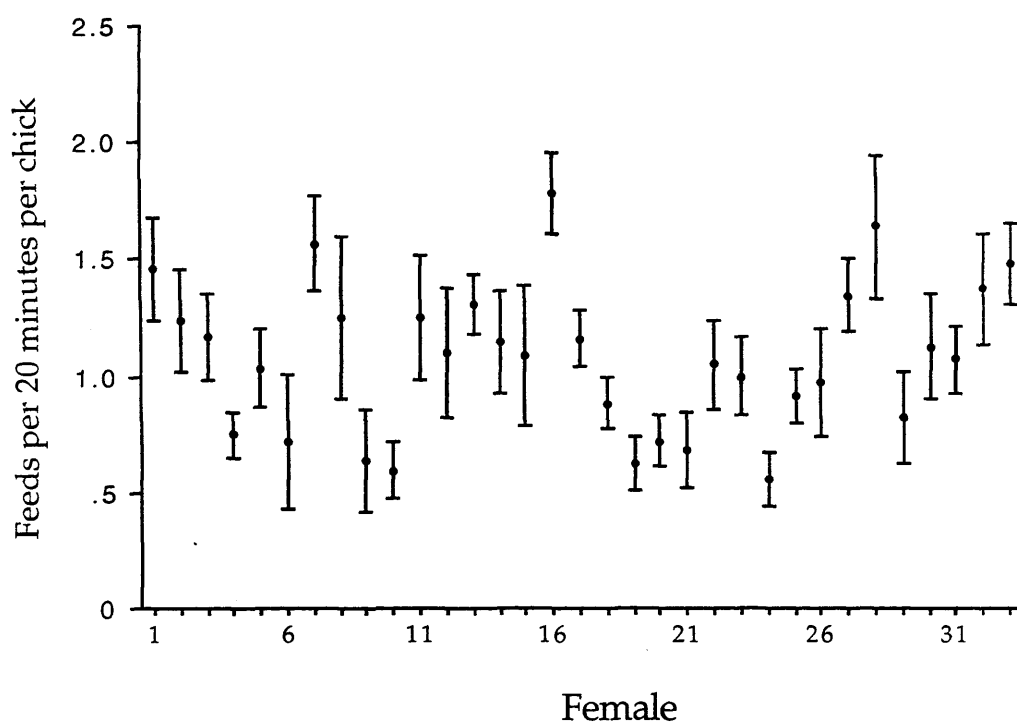
3.4.1 Male feeding rate

We found no evidence of a positive relationship between male badge length and either the absolute rate of provisioning (Figure 3.3a; $r^2 = 0.03$, n = 29, p > 0.25) or the rate of male provisioning visits per chick (Figure 3.3b; $r^2 = 0.005$, n = 29, p > 0.5). In fact, both these relationships were negative - indicating that large badged males fed at a lower rate - but not significantly so.

3.4.2 Female feeding rate

There was no relationship between the size of the badge of a female's partner and the female's absolute provisioning rate (Figure 3.3c; $r^2 = 0.07$, n = 29, p > 0.10). However there was a significant positive relationship between the size of the badge of a female's partner and her rate of chick-feeding in terms of feeds per chick (Figure 3.3d; $r^2 = 0.15$, n = 29, p < 0.05).

Figure 3.3 Relationship between male badge size and male and female chick-feeding rates. (a) Absolute male chick-feeding rate against badge length. (b) Male chick-feeding rate per chick against badge length. (c) Female absolute chick-feeding rate against the badge length of her pair male. (d) Female absolute chick-feeding rate per chick against partners badge length. (r^2 refers to linear correlation coefficient, p refers to associated two-tailed probability) all rates are measured in visits per hour.

a)

Male badge length (mm)

b)

$r^2 = 0.01$
n = 29
p > 0.50

(x-axis) Male badge length (mm)
(y-axis) Male feeding rate per chick

c)

$r^2 = 0.07$
n = 29
p > 0.10

(x-axis) Pair male badge length (mm)
(y-axis) Female feeding rate

d)

$y = 0.275x - 5.840$

$r^2 = 0.15$
$n = 29$
$p < 0.05$

Female feeding rate per chick

Pair male badge length (mm)
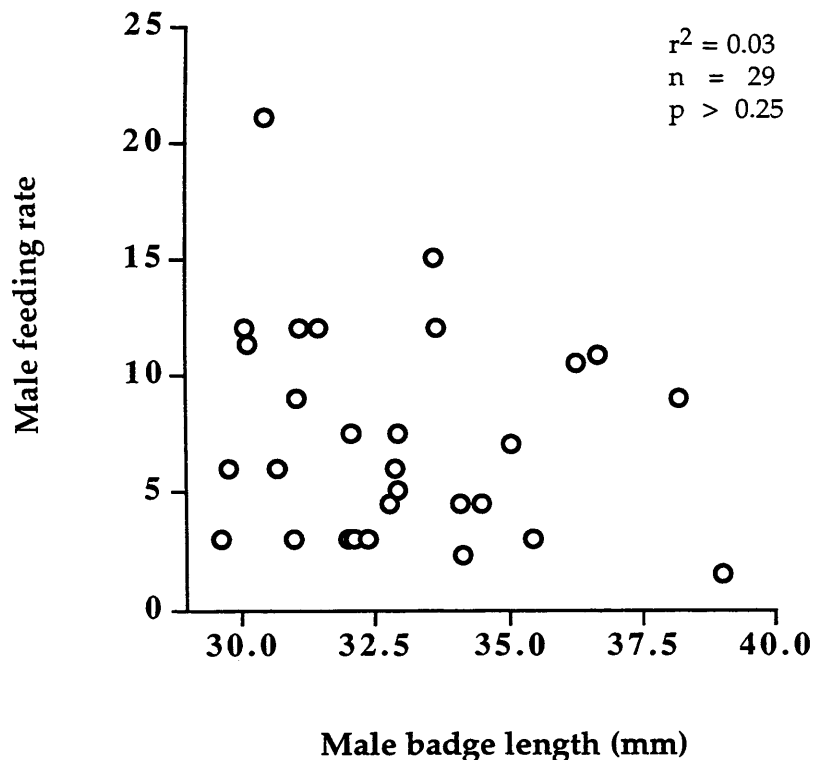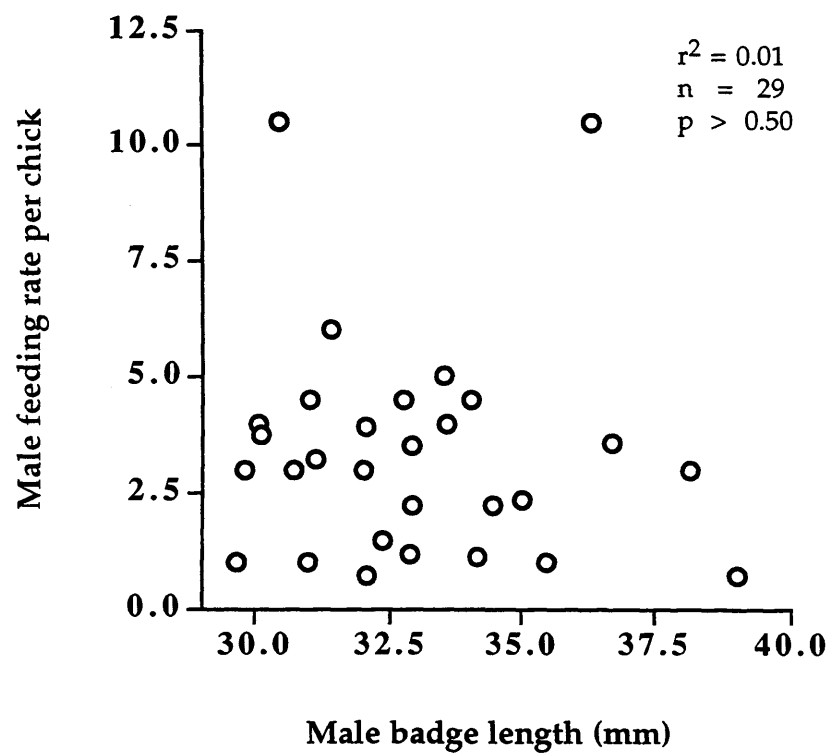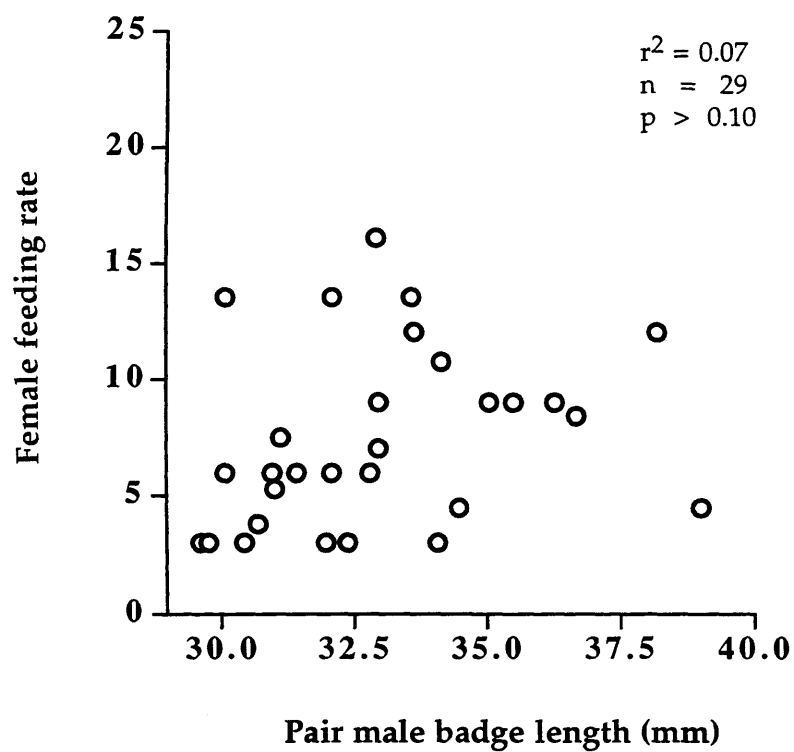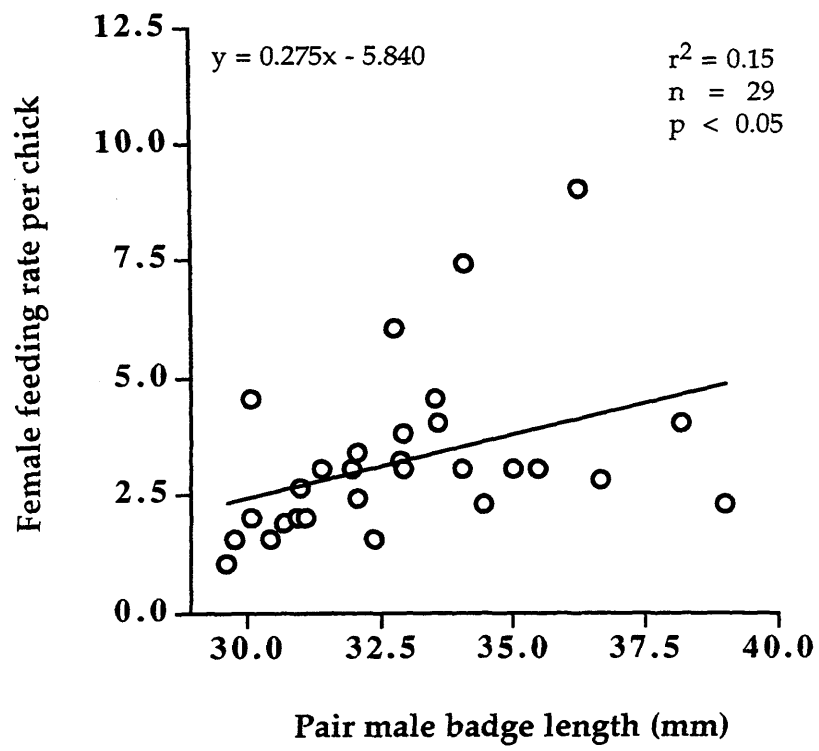
3.4.3 Pair provisioning rate

There was no relationship between the total feeding rate per chick, of the pair and male badge size (Figure 3.4; $r^2 = 0.02$, n = 29, p > 0.25). Hence the total rate of feeds received by each chick was not related to the badge size of its father.

Figure 3.4 Relationship between male badge length and the total number of chick feeds per chick per hour. r refers to linear coefficient, p refers to associated two-tail probability.

Male badge length (mm)
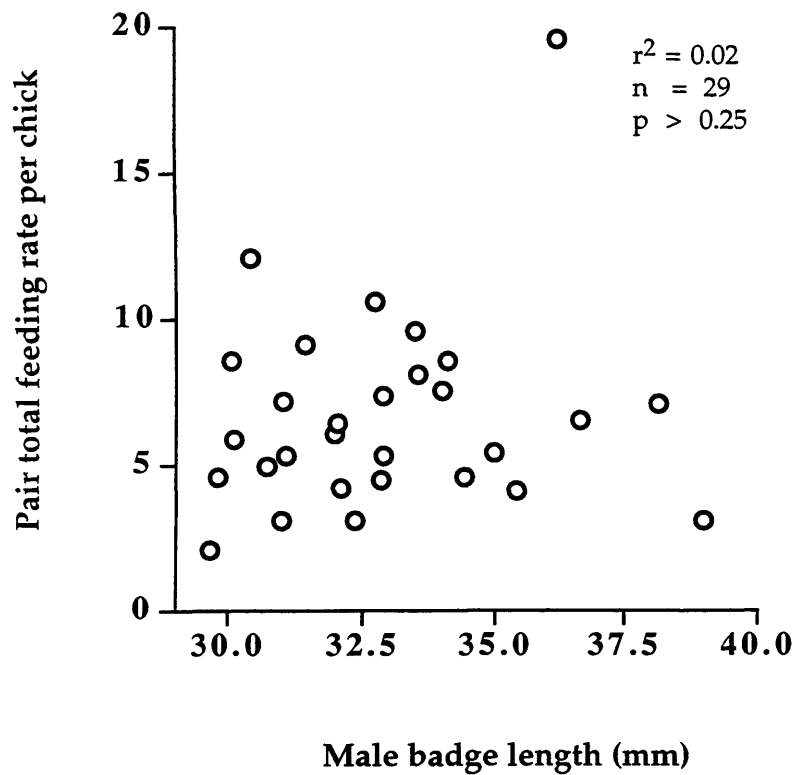
3.4.4 Relative male provisioning rate

When male provisioning effort was measured as the proportion of total chick-feeds that were provided by the pair, there was a significant negative relationship between the male badge size and male provisioning effort (Figure 3.5; $r^2 = 0.19$, n = 29, p < 0.05).

Figure 3.5 Relationship between male badge length and the relative rate of chick feeds as a proportion of the pair total feeding rate. r^2 refers to linear coefficient, p refers to associated two-tail probability.
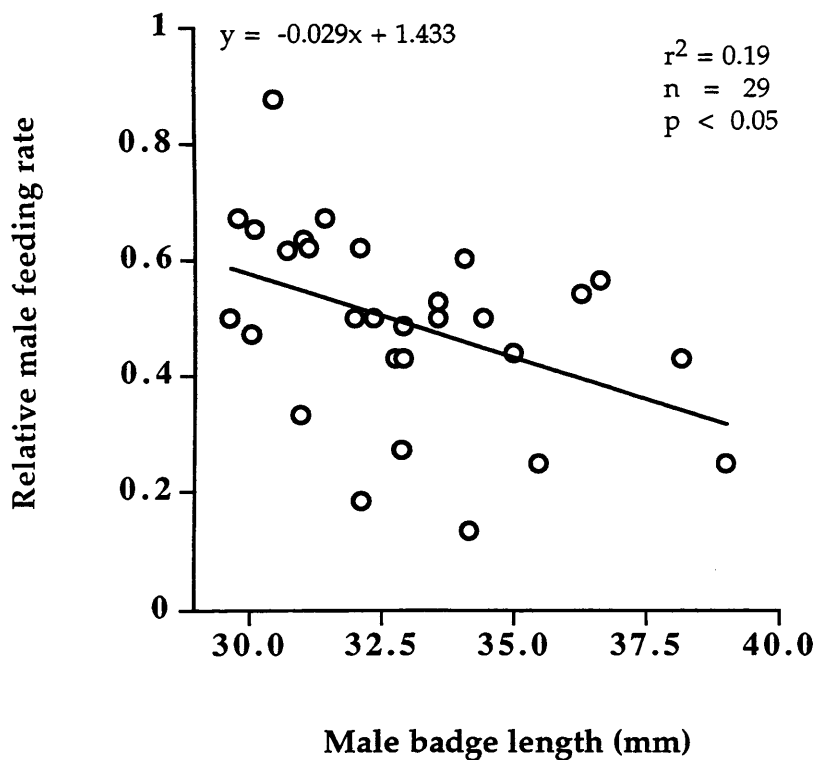
3.5 Discussion

We found no support for the good parenting hypothesis in the Lundy Island population. Male house sparrows with large badges, which are assumed to be 'sexy' (Møller 1988, 1989, 1992; Maynard Smith & Harper 1988; Wetton et al. 1995; Veiga 1993) did not provide more chick feeds. Indeed, in terms of their contribution relative to the female, large badged males actually provided less care than small badged males. Not only do we find no support for the good parenting hypothesis (Hoelzer 1989; Heywood 1989), our results suggest that in this population of house sparrows there appears to be a bad parent effect, (but see Møller (1989) for qualitative suggestion that badge size may be correlated with feeding rate in a Danish population).

Why would females choose showy males as partners when on average, they tend to provide less care for their offspring? Particularly as it seems that females must then compensate for any shortfall in male care (Johnstone 1996; Kilner 1997).

The traditional explanation for such behaviour is the differential allocation hypothesis, which suggests that a female paired to an attractive mate will provision at a high rate in order to maintain that mate (Burley 1988), or alternatively, females will invest more in their offspring as they will be repaid in terms of the higher genetic quality of those offspring (de Lope & Møller 1993; Petrie & Williams 1993). The differetial allocation hypothesis is very much a female led phenomenon. As a female increases her effort her partner will be able to decrease his. An alternative way of interpreting the same result is through the 'lazy male' process.

The 'lazy male' process is driven by males being lazy as opposed to females working harder. Under this explanation, large badged males are lazy because they can afford to be, confident of their 'sexiness'; they will always be assured of finding mates and the risk of desertion is low as they are in demand. Females are forced to pay the price of seeking the best genes by having to invest greater effort in provisioning. Of course, the relative costs and benefits of reduced parental care versus 'good genes' to overall fitness of the offspring will play a vital role in the feasibility of this process. Although there is currently no empirical proof for the lazy male process, there is evidence of several mechanisms through which it could be maintained. Firstly, Gustafsson et al. (1995) revealed, through an experimental manipulation of reproductive effort in the collared flycatcher *Hypoleuca albicollis, a*

relationship between the effort invested in reproduction in one year and the size of a sexually selected trait (forehead patch), the following year. This type of trade-off could maintain a lazy male process, with the most ornamented males reducing parental care in order to maintain their status. Females paired to these males would be willing to make up the deficit with the assurance that their offspring sired by these males would probably have good genes (Sheldon et al. 1997). Of course such a system would rely on the honesty of the sexual ornament.

An alternative, and more simple mechanism for maintaining the lazy male process would be a physiological trade-off between the sexual ornament and feeding behaviour. Hegner & Wingfield (1987) showed through an experimental manipulation of testosterone levels in male house sparrows that those males with increased levels of circulating testosterone fed their offspring at a significantly lower rate than control males. These males also indulged in higher levels of social activity with other males away from their nest. Whilst it was originally thought that badge size in house sparrows was unrelated to testosterone level (Keck 1934) it has recently been found in another study that a positive relationship may exist (S. Norris & A. Goldsmith pers. comm.). If this proves to be true then it is possible that males are forced into a physiological trade-off between maintaining their status and chick-feeding. The combination of both of these effects together would be consistent with the predictions of the lazy male hypothesis.

The 'lazy male' process remains to be tested by the manipulation of male traits during the chick rearing phase of reproduction. If there is no change in relative provisioning rates after a badge size manipulation then the female is obviously not responding to her partners 'sexiness' as suggested by the differential allocation hypothesis.

Regardless of the precise mechanism driving increased female investment in chicks fathered by attractive males, it appears that the 'good parent' hypothesis has little power in explaining the maintenance of either female choice, or male ornaments in the Lundy Island population of house sparrows. If females do prefer those males with the largest badges as suggested by Møller (1988, 1989) we can find no evidence of a direct benefit from this preference with regard to chick-feeding, arguably the most likely direct benefit to be gained from a male house sparrow. However, it is possible that there are other, more subtle, direct benefits that may still be gained. The failure of the good parenting model to explain female preference for large-badged males leaves

several alternatives. Firstly there are other direct benefits that lead to higher fecundity, and then the indirect benefits such as the good genes hypotheses. Finally the possibility remains that females do not actually show a preference for a particular male phenotype.

CHAPTER FOUR

Do females paired to large-badged males have higher reproductive success?

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CHAPTER FOUR

Do females paired to large-badged males have higher reproductive success?

4.1 Abstract

It is widely assumed that there will be a positive relationship between the size of a sexually selected trait and reproductive success. However, most studies of the relationship between trait size and reproductive success are based on indirect measurements of reproductive success such as the date of the first clutch. Here, we present data from a field study of house sparrows on the actual numbers of eggs laid, chicks and fledglings produced as well as following these through to recruitment. We found that for every measure, reproductive success was negatively correlated with the size of a sexually selected trait. Hence, females mating with 'sexy' males do not gain a fecundity advantage. This suggests that other mechanisms such as 'good genes' may be responsible for maintaining female preferences for 'large' ornaments.

4.2 Introduction

Since costly sexual ornaments were first linked to non-random mating (Darwin 1871), there has been a great deal of interest in the origin and maintenance of such traits (e.g. Wallace 1889; Morgan 1903,1932; Huxley 1914,1938; Fisher 1915,1930; Maynard Smith 1958,1991; O'Donald 1962; Lack 1968; Cambell 1972; Lande 1980; Bradbury & Andersson 1987; Andersson 1994). The most engaging question being, why should females prefer males with elaborate ornaments? Currently, there are two main sets of ideas (see Andersson 1994). The 'good genes' hypotheses predict male sexual ornaments to reflect favourable genes that may be passed onto their offspring; genes for increased viability (Williams 1966, Hamilton & Zuk 1982), or genes for increased attractiveness (Fisher 1915, 1930). Alternatively, the 'direct benefit' hypotheses (Hoelzer 1989, Kirkpatrick & Ryan 1991) predict that male ornaments will reflect tangible benefits that females thus acquire, for example, territory (Alatalo 1986), food 'gifts' during incubation (Nisbet 1973), provisioning of nestlings (Linville et al. 1998).

Fundamentally, both good genes and direct benefit models predict, all else being equal, a positive relationship between the size of sexual ornaments and reproductive success. However, despite the amount of work on sexual selection that has been carried out on a great number of socially monogamous birds, there have been very few demonstrative tests of this prediction. To date, perhaps the only strong evidence for a positive relationship between trait expression and fecundity is that provided by Møller (1994) in the European barn swallow, *Hirundo rustica* in which it has been demonstrated that males with the longest tails produce more offspring than their shorter-tailed counterparts. This result is largely caused by those males with long tails returning to the breeding area earlier, and subsequently managing to produce two clutches, twice as many as their later arriving, shorter-tailed counterparts. When this work was repeated on the same species, but in North America, there was no difference in reproductive success between long-tailed males and those with shorter tails (Smith & Montgomerie 1991) largely because all pairs had only one clutch.

The general lack of evidence for a relationship between variation in sexual traits and variation in fecundity could be due to a lack of tests, or a bias in the acceptance and publication of negative results (see Alatalo et al. 1997). The lack of tests could be caused by the difficulty of adequately measuring reproductive success. A good measure of reproductive success must ideally account for the total genetic production of individuals through the accurate assignment of all extra-pair offspring to their fathers (e.g. Sundberg & Dixon 1996; Yezerinac & Weatherhead 1997); and also, accurately measure production and survival of offspring, ideally up to recruitment into the breeding population. The latter can generally be achieved with a closed population, wherein individual birds can be monitored throughout their lives (e.g. Grant & Grant 1987; Smith 1988; Kikkawa 1986; Gustafsson & Sutherland 1988).

Our study population of the house sparrow is remarkable because it shows a negligible level of immigration and emigration (Section 5.3). It is very rare to have a population isolated to this extent, in which there is no natal dispersal away from the study area (see Smith 1988), important for an accurate measurement of reproductive success. Additionally, in our population there is a very low level of extra-pair paternity (< 1 %), and no recorded intra-specific brood parasitism (Chapter Two) this means that we only have to account for within-pair reproductive success in our assessments. The combination of these features in our population allowed us to monitor true total reproductive success and test the predicted relationship between reproductive success and

the size of a sexual ornament. The black throat patch, ' badge', of the house sparrow has previously been shown to be under sexual selection, with large badges adjudged to be attractive by females in the choice of social and sexual partners (Møller 1987, 1988; but see Kimball 1996). We used variation in this sexually selected trait to examine the following questions. Is variation in badge size correlated with (i) an earlier start to breeding, (ii) greater within-nest productivity, or (iii) higher levels of offspring recruitment to the breeding population?

4.3 Methods

4.3.1 Study population

This study was carried out between January 1995 and July 1997 on Lundy Island, 15 km off the south west coast of England (51.11 N 4.40 W). (For further details of the study site see Section 1.3.2). Adult birds were caught on multiple occasions throughout the study and all adults in the population were colour-banded with unique colour combinations. Morphological measurements were taken on several occasions throughout the study (Section 3.3.2), all of which were found to be highly repeatable within a single adult moult. Badge length was measured using callipers, at the base of the black throat patch feathers, directly from captured birds in the hand. During the breeding season this 'hidden' area is highly correlated with the area of the visible badge ($r^2 = 0.47$ p < 0.001 n $= 47$) (also Møller 1987, Veiga 1993). This measurement is highly repeatable throughout the whole year, not just when the buff tips have worn off ($r = 0.755$, $F_{12,13} = 7.778$, p < 0.001; calculated after Falconer (1960)). The body condition index (BCI) used is the residual from a linear regression of body mass and tarsus length.

All breeding attempts were in nest boxes. During the breeding season (April-August) all possible nest sites were monitored every two days for signs of nesting. Once egg laying had begun, close monitoring of the nest commenced and continued until fledging (Section 5.3.2). Chicks were measured, ringed, and colour-banded at 12 days old and were then monitored for post-fledging survival.

There is a limited amount of habitat suitable for house sparrows to breed in on Lundy Island, and it was possible to seek out all possible nesting sites and check for breeding attempts, this is critical for a proper evaluation of total reproductive success of all individuals. Although over 90% of pairs nested in nestboxes, some did nest successfully in roof spaces and cavities in walls, in those cases where access to the nest was impossible, monitoring of breeding was not as intensive and these pairs were excluded from parts of the analysis. In 1996, all breeding attempts by pairs were detected, however some males which remained unpaired were more elusive and remained undetected. The analysis is conducted on individuals which had a least one reproductive event.

4.3.2 Estimating reproductive success

Approximately 90% (92/102) and 100% of (105/105) all breeding attempts on the island were in nest boxes and therefore monitored in 1995 and 1996, respectively. In each case, the number of days to the first egg laid were calculated from 1st May. Once laying has started, house sparrows lay an egg every day until the clutch is complete (Summers-Smith 1963). By checking nests every two days we were able to work out when breeding began and predict a hatching date assuming that incubation starts on the day the clutch is completed and lasts 11 days (Summers-Smith 1963). Hatching success (eggs laid/ eggs hatched) was monitored and any unhatched eggs were carefully opened after 12 days incubation and assessed as to the approximate size of the failed embryo within. The number of fledglings is the number of chicks alive on day 12; chicks that survive to this age all fledge successfully as confirmed by the absence of corpses in the nest five days later. The nests were not inspected between day 12 and 17 due to the possibility of chicks leaving the nest prematurely. Clutch size (number of eggs laid), number of chicks, and number of fledglings were used to quantitatively measure reproductive success.

Although all data was collected from both 1995 and 1996 the majority of analyses used only data from 1996. During 1995 an experimental brood manipulation was being conducted (Section 5.3.2). As we are studying the relationship between badge size and natural reproductive success it would have been inappropriate to use data from 1995. The only data that we could use from 1995 is that for first egg date which occured before any manipulation and therefore will not be affected. Six pairs were excluded from the analysis due to anthropomorphic 'disasters' (for example human disturbance causing desertion, or damage to nestbox) affecting their reproductive efforts. Three males were found to be breeding polygynously, these were also excluded.

Data was tested for departures from normality using the Lilliefors test (Wilkinson 1992). Residuals of regressions were also checked for normality, in both cases a probability of ≤ 0.05 was taken to indicate biological significance. Linear regressions were carried out using the STATVIEW package. Logistic regressions were carried out using the SYSTAT package (Wilkinson 1992).

4.3.3 Measuring chick survival

By creating a model based on real data from a small sample of chicks in the nest and their actual survival, we were able to predict the likelihood of any

chick surviving to recruitment based on morphological measurements in the nest at 11 days old, this allowed us to remove stochastic effects on survival and analyse data from 1996 despite not having accurate measures of survival from 1997. From hatching, chicks were measured periodically and marked by clipping one claw (different one for each chick in a brood), until day 11 when they were ringed with a metal ring (BTO) and a unique combination of colour rings. From fledging, the survival of chicks was monitored alongside that of the adults (Section 5.3.3). One hundred and forty two chicks were used in the analysis. After being measured at 11 days old their subsequent survival was monitored up to and through recruitment into the breeding population twelve months later.

4.3.4 The measurement of offspring quality

Logistic regression was used to analyse offspring quality and survival (McCullugh & Nelder 1983; Crawley 1993). Following Coulson et al. (1997) we measured 'recruitment' as survival of offspring to the next breeding season. Survival of chicks was described as a binary variable, with 1 representing animals that died before May 1st of the year following hatching, and 0 describing those that survived to be recruited into the breeding population. We used a logistic regression model into which, the inclusion of terms (number of siblings, tarsus length and weight at age four days and 11 days, hatching date, and parental characteristics) was based on tests of reduction in the residual deviance. Reduction in residual deviance is distributed approximately as χ^2, with degrees of freedom equal to the number of additional parameters fitted. Deviance is a measure of the goodness-of-fit of a model and is the logarithm of the ratio of two likelihoods. The proportion of chicks that died per combination of terms included in the model was linearized by the logit function, a logarithmic transformation of the odds ratio,

-1*(survival*log(estimate)+(1-survival)*log(1-estimate)

Using non-linear regression with a maximum likelihood loss function (see above) in the SYSTAT statistical package we explored the relationship between survival and nestling characteristics in the nest. We investigated the relationship between residual weight of chicks in the nest and subsequent survival because other studies have revealed this characteristic to be highly related to quality and survival and therefore of predictive value (Gustafsson & Sutherland 1988). As given here, the residual weight of a chick is derived from the regression of tarsus length on body weight (dependent variable). The

relationship between tarsus length and body weight is highly significant (p < 0.001, n = 125, r = 0.7).

The residual weight was found to show a significant relationship with survival:

(survival=exp(A+B*resid. weight)/(1+exp(A+B*resid.weight))

(d.f.=141, In this model, A = 2.18, s.e. is 0.259, p < 0.001, B= -0.278, s.e. = 0.135, p=0.05 Figure 4.1)

Figure 4.1 Predicted survival up to recruitment into the breeding population as modelled by the residual weight of 11 day old chicks in the nest
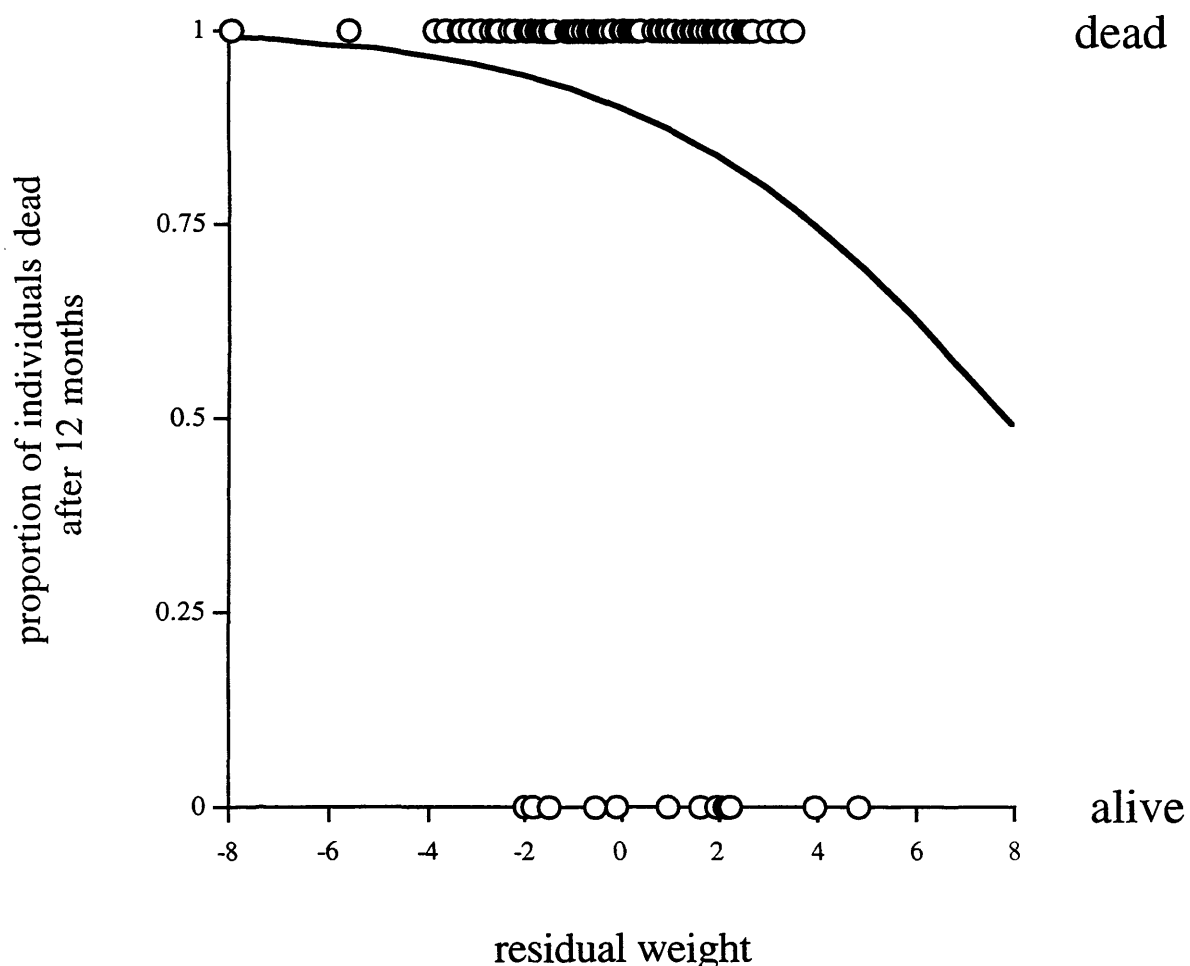
From this model we were able to use residual nestling weight to establish the likelihood that a particular nestling would be recruited into the breeding population. The above model allowed us to predict, from their weight in the nest, the likelihood of chicks surviving to recruit into the breeding population, the removal of other stochastic effects on survival gave us a

sample size large enough to thoroughly investigate the relationship between badge size and number of recruits produced.

4.4 Results

4.4.1 Badge size versus first egg date

In both years the there was some synchronisation of breeding within the population although the total variation in date of first egg was spread over half the duration of the whole breeding season. Initially, this can give the impression that some of the later first clutches are actually very early second clutches. This is definitely not the case because all birds were still coming into reproductive condition in May and there were no old nests or fledglings on the island. There was a significant positive relationship between badge size and the first egg date, males with smaller badges breed earlier than those with big badges (Fig 4.2; spearman rank correlation coefficient = 0.27, n = 62, p < 0.04 two tailed).

Figure 4.2 The relationship between badge length of the male and the first egg date of the pair. The two clusters do not represent second clutches, all points represent first breeding attempts by individuals (see text).
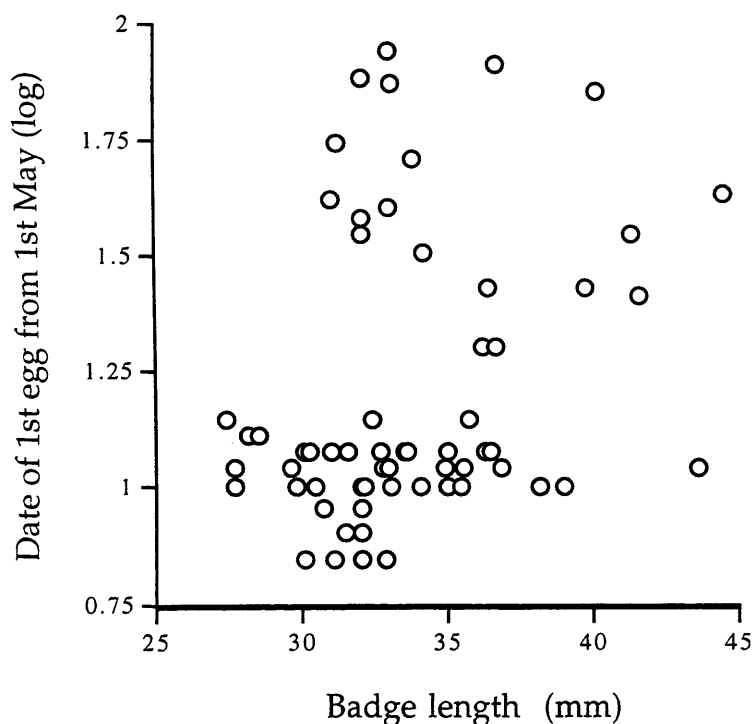
This result contrasts strongly with the finding by Møller of a negative relationship between male badge size and the date of the first egg (Møller 1988, 1990). In this analysis some individuals are represented twice, once for 1995 and once for 1996. This is justifiable because the prediction being tested is that there is a relationship between badge size and breeding date, because badge size changes from year to year even if an individual is represented in the analysis twice i.e. from 1995 and again in 1996 the badge size will be different.

4.4.2 Badge size versus production of offspring

The number of offspring a male produced was analysed at three stages of the breeding cycle; numbers of eggs, number of chicks in nests, and number of fledglings produced. In contrast to the prediction, there was a negative relationship between each of these measures of male reproductive success and the size of a male's badge (Fig 4.3 a-c) (see Table 4.1). When we tested for a relationship between these reproductive variables and other male characteristics including tarsus length, wing chord, body mass and BCI, no relationship was found (see Table 4.1).

Table 4.1 Relationships between four measures of male reproductive success and male morphometric characters (BCI = residuals from a linear regression of tarsus length and body mass) No. of recruits is actually no. of predicted recruits. Values are r^2 resulting from linear regression. Levels of significance denoted as follows where applicable * $p < 0.05$, ** $p <$ 0.005

dependent variable	Male characteristics (independent variables)				
	Tarsus length	Wing chord	Weight	BCI	Badge length
no. eggs (n=24)	0.005	0.034	0.005	0.049	-0.147
no. chicks (n= 24)	0.022	0.018	0.007	0.100	-0.130
no. fledgings (n=28)	0.017	0.073	0.018	0.068	-0.183*
no. recruits (n=29)	0.070	0.051	0.015	-0.111	-0.290**

Figure 4.3 Relationships between pair male badge length and direct measures of reproductive success.

a) Number of eggs against badge length

$r^2 = 0.15$
$n = 24$
$p < 0.1$
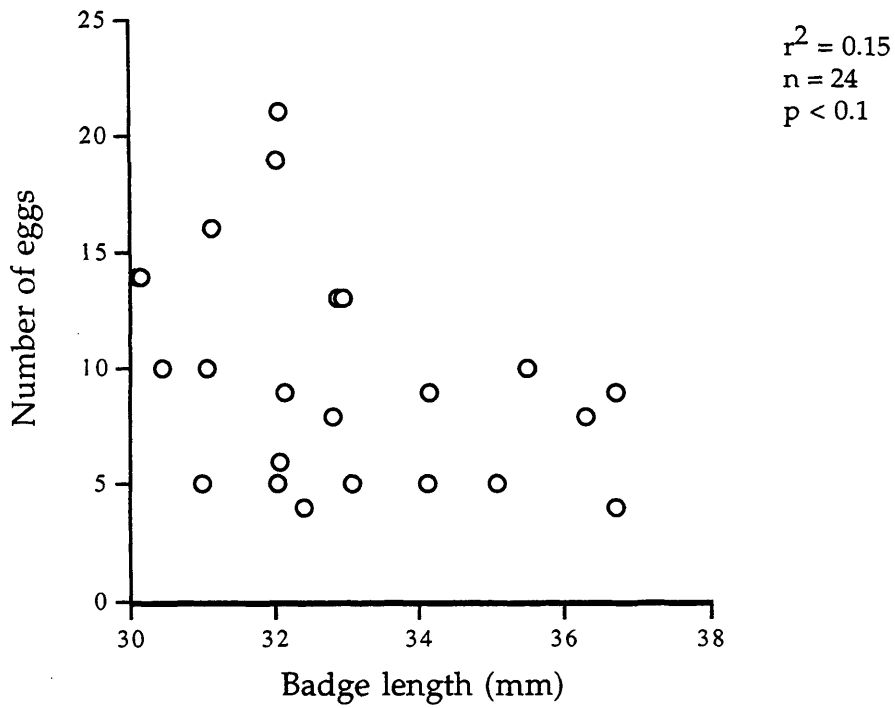
b) Number of chicks against badge length

$r^2 = 0.13$
$n = 24$
$p < 0.1$

57

c) Number of fledgings against badge length

$y = -0.607x + 24.952$

$r^2 = 0.18$
$n = 28$
$p < 0.05$

Number of fledglings (y-axis, 0 to 15)

Badge length (mm) (x-axis, 30 to 38)
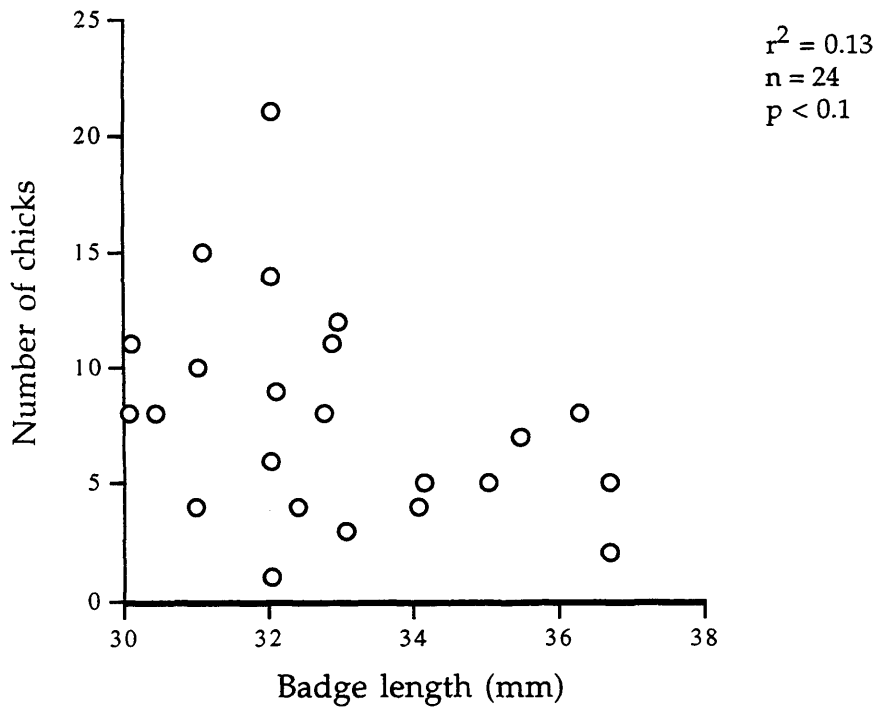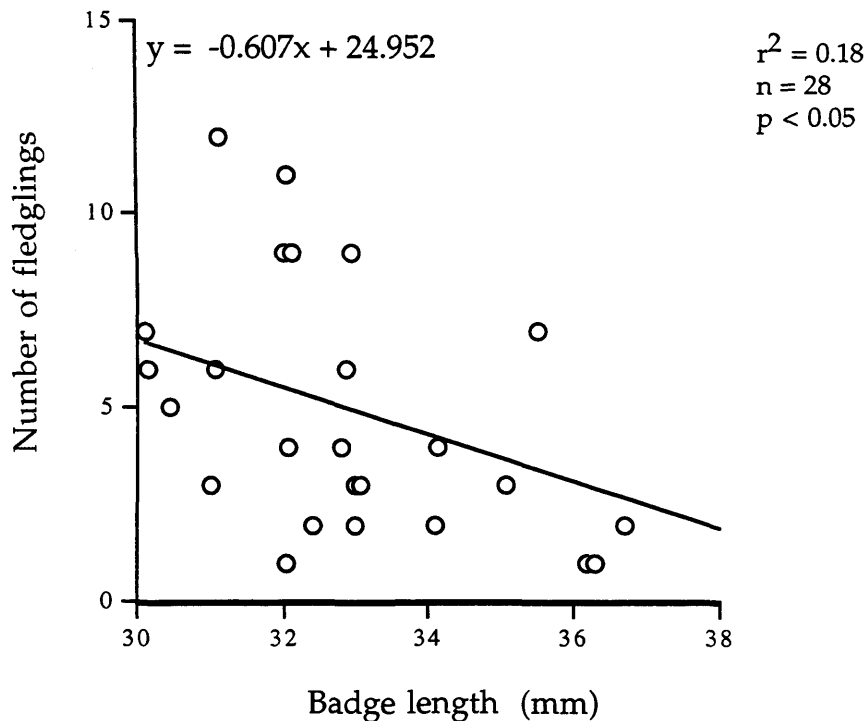
4.4.3 Badge size versus production of recruits

Using the binomial log-likelihood model (Fig 4.1), the number of recruits a male was predicted to produce was strongly negatively correlated with his badge size. Males with large badges were shown to have fewer predicted recruits than those with smaller badges ($r^2 = 0.29$, $n = 28$, $p = 0.003$)(Figure 4.4). The predicted number of recruits did not show a significant relationship with any other male characteristic measured except a weak relationship with the BCI (Table 4.1). When badge length and the BCI were put into a multiple regression they explained nearly half the variation between males in the predicted number of recruits ($n = 25$, $r^2 = 0.45$ $p = 0.002$) and both variables were independently correlated with the number of recruits produced (Table 4.2).

Figure 4.4 The relationship between male badge length and the number of offspring recruited into the breeding population predicted by a model based on actual survival and residual weight of chicks in the nest (see text).

$$y = -0.088x + 3.436$$

$r^2 = 0.29$
$n = 29$
$p < 0.01$
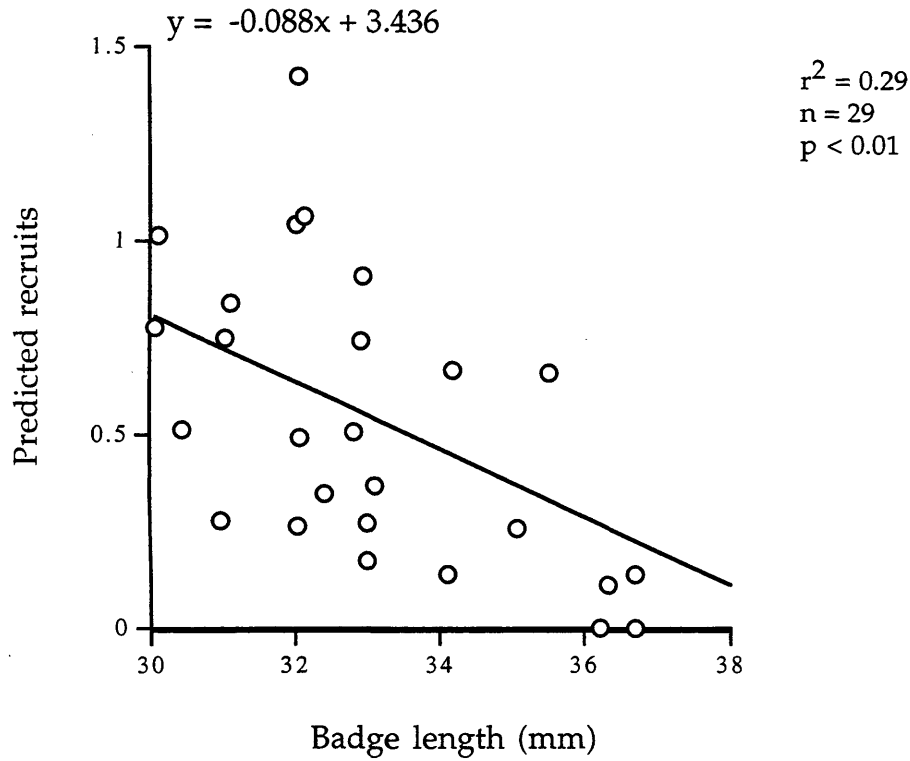
Badge length (mm)

Table 4.2 Multiple regression of the relationship between the predicted production of recruits and two male characteristics.

	slope (±SE)	t- value	f- value	p
Intercept	3.44 (0.87)	3.94	15.53	0.001
Badge length	-0.09 (0.03)	-3.37	11.34	0.003
BCI	0.10 (0.04)	2.16	4.68	0.042

$n = 25$ $r^2 = 0.45$ $p = 0.002$

4.5 Discussion

Contrary to the predictions of the 'direct benefits' and 'good genes' hypotheses, (Kirkpatrick & Ryan 1991; Williams 1966) males with the largest sexual ornaments did not have the highest reproductive success. In fact, badge size was negatively correlated with all measures of reproductive success. Females paired with large-badged males laid fewer eggs, subsequently produced fewer chicks and fledglings and are predicted to recruit fewer offspring into the breeding population.

Why do the males with the largest badges, usually assumed to be 'sexy' (Møller 1987, 1988, 1989; Veiga 1993; Wetton et al. 1995) have lower reproductive success? Furthermore, why should females favour males as partners that will lead to a low reproductive success? Several non-mutually exclusive explanations could account for this apparent paradox.

First, large-badged males, or females paired to them, might achieve higher lifetime reproductive success if there is a trade-off between survival and reproduction (Williams 1966; Gustafsson & Sutherland 1988). A low within-season reproductive effort could be adaptive if it resulted in a higher probability of surviving to breed in successive seasons.

Second, females could gain a net benefit from pairing with a large-badged male if the relatively few offspring produced are of proportionately high genetic quality. For instance, large-badged males may carry beneficial genes for either, viability during adulthood e.g. parasite resistance (Hamilton & Zuk 1982), or sexiness (a genetically determined large badge) (Fisher 1930; Williams 1966). Fit offspring will confer indirect fitness on their parents (Weatherhead & Robertson 1979).

Third, the result could be confounded by an age-related element to badge size. Veiga (1993) showed that badge size is positively related to age. A decline in annual reproductive success with advancing age has been demonstrated in the sparrowhawk, *Accipiter nissus* (Newton 1997) and the Seychelles warbler, *Acrocephalus sechellensis* (Komdeur 1996). The observed relationship between a large badge and low reproductive success could be due to the confounding effect of old males having low reproductive success and also a large badge. Whilst possible, this will not fully explain the paradox that females have low reproductive success with these males, unless in

combination with the good quality effects as above; old males being of high quality.

Fourth, in monogamous systems reproductive success may be divided into within-pair, and extra-pair reproductive success. An adaptive trade-off between these two components may lead to the observed result. Through the diversion of time and resources towards the gaining of extra-pair paternity, males may increase extra-pair reproductive success at the cost of a reduction in within-pair reproductive success (Raouf et al. 1997; but see Weatherhead & Boag 1997). Through such a trade-off, a male may increase his overall reproductive success. Extra-pair paternity does occur in the house sparrow, with the levels reported from three other populations falling between 13% and 20% (Wetton et al 1992; Kimball 1995; I. Stewart pers. comm.). However, the level of extra-pair paternity on Lundy was insignificant (less than 1%, Chapter Two). Despite this low level, extra-pair copulations do take place and it would be surprising if males do not still attempt to gain extra-pair copulations even given the fact that they rarely lead to extra-pair fertilisations.

If females do prefer to pair with large-badged males, despite the consequent reduction in their annual reproductive success then we must assume that they gain some benefit from pairing with these males, otherwise surely it would be maladaptive. To explain the variation in badge size and its relationship with reproductive success we are left with two alternatives. An adaptive trade-off between current and future reproduction (Williams 1966; Stearns 1989), and the good genes theory (Williams 1966; Weatherhead & Robertson 1979; Hamilton & Zuk 1982), whereby a female is prepared to trade-off numbers of offspring for quality. These hypotheses are further explored in Chapter Five and Chapter Seven.

CHAPTER FIVE

The cost of reproduction in the house sparrow: the effect of an experimental brood manipulation on adult survival

5.1 Abstract

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    5.3.1 The study

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CHAPTER FIVE

The cost of reproduction in the house sparrow: the effect of an experimental brood manipulation on adult survival

5.1 Abstract

There are many trade-offs associated with reproduction in monogamous birds, here we examine just one, the cost to adult mortality of reproductive effort. If it exists this trade-off will obviously have a great implication on individual life history. This was investigated using an experimental manipulation of brood size to dissociate the effects of differing parental resources and natural clutch size, essential to establishing a causative relationship between reproductive effort and mortality. It was found that female house sparrows with artificially enlarged broods did suffer higher mortality over the subsequent year, the effect was not significant in males. This sex-specific result probably reflects a fundamental difference between the sexes in passerine birds.

5.2 Introduction

Trade-offs are interesting because they are a major cause of life history variation both between species and within a species. They are one of the fundamental processes underlying both natural selection and sexual selection (Williams 1966; Stearns 1989). Of great importance to a full understanding of sexual selection and one of the most basic trade-offs is that between fecundity and survival. Higher reproductive effort in one year is predicted, and has been demonstrated to have a deleterious effect on subsequent condition and reproduction (e.g. in the Canada goose *Branta canadensis*, Lessells 1986; blue tit *Parus caeruleus*, Nur 1984,1988; rook, *Corvus frugilegus*,Røskaft 1985; pied flycatcher, *Hypoleuca ficedula*, Askenmo 1979; the glaucous-winged gull, *Larus glaucescens*, Reid 1987 and the kestrel, *Falco tunninculus*, Daan et al. 1996). The existence of a trade-off between reproduction and survival can only be established through an artificial manipulation of reproductive effort.

Simple observations may not spot a trade-off because some individuals have access to more resources than others, hence rich individuals can survive and reproduce better than poor individuals, even though there may be a trade-off between the two (Reznick 1985).

The aim of this study is to assess the trade-off between current and future reproduction in the house sparrow, *Passer domesticus*. The major component of future reproduction in the house sparrow will be overwinter survival; you have to be alive to reproduce. With the right population this measure is relatively easily obtained.

5.3 Methods

5.3.1 The study

The population of house sparrows studied was on Lundy Island, which lies in the Bristol Channel and is 20 km from the nearest mainland (English) coast. This closed population is ideal for studying individual survival due to very low levels of immigration and emigration. Records from the bird observatory on Lundy in the 1950's and 1960's, when there were no resident sparrows present on the island, suggest a very low level of immigration (less than two individuals every three years)(Journals of the Lundy Field Society 1947-1997). There is no reason to believe that this level has increased, particularly as the population on the mainland has declined in recent years (Glue 1994). Also, despite many years ringing on Lundy, no island-ringed bird has ever been relocated on the mainland (British Trust for Ornithology pers. comm.). We can assume, therefore, that individuals which disappear from the population have indeed died.

The manipulations were carried out in the breeding season of 1995 and survival of the whole population was monitored thereafter to the summer of 1996. One hundred per cent of the adult male house sparrows and over 90% of the females present during 1995 were caught and each was given a unique combination of three plastic colour rings and a single coded metal ring (supplied by the British Trust for Ornithology).

5.3.2 Breeding and the manipulation

Approximately 40 pairs breed on the island with over 90% habitually using nestboxes. The population breeds synchronously which allowed us to swap broods of chicks randomly on the day of hatching, thus removing any effects of egg production and incubation (Monaghan & Nager 1997). Following the manipulation, all broods were monitored as to the outcome of the reproductive event.

The majority of pairs on Lundy had two broods in the 1995 season and manipulations were performed on both broods. The manipulations were an incidental side-effect to a cross-fostering experiment as described in Chapter 7. This accounts for the uneven distribution of the different experimental groups. The analysis was conducted using the total experimental manipulation an individual was subject to over the whole season. The mean brood size in 1995 was 3.61 chicks (std dev. 0.84) with the mean total number of chicks from all broods being 5.67 chicks (std dev. 0.35). The experimental brood size manipulation ranged from the natural total brood size to minus two and plus two this amount (14 individuals had a brood enlargement, 18 underwent a reduction). The 46 males and 34 females who were either not manipulated, or underwent a total manipulation of zero will serve as a control group and represent the natural level of survival for individuals in this population. The brood manipulations were independent of male badge size ($r^2 = 0.009$, n = 46 p > 0.5). No broods were increased or decreased beyond the naturally observed brood sizes (range 2-7). Sample sizes are uneven (females n = 13, males n = 19) due to some females remaining unringed during the early part of the study. The criteria for survival was the presence of a bird at the start of the breeding season of 1996.

5.3.3 The measurement of Survival

Survival was monitored by conducting extensive visual surveys at areas frequented by the whole population (e.g. feeding areas, dust baths, roost sites). All extant individuals were recorded on multiple occasions during each survey, indicating that coverage of the whole population was complete. Individuals not sighted during a survey were adjudged to have died; this assertion was valid because individuals not recorded in a particular survey were never sighted thereafter.

The Fisher exact test (Siegel & Castellan 1988) was used to test the null hypothesis that 'treatment' (increase versus decrease of reproductive effort) did not affect survival.

5.4 Results

Overall, there is an effect of the experimental manipulation, with individuals having their natural brood size increased suffering significantly higher mortality in the subsequent winter (Fisher exact two-tailed probability = 0.036). The Fisher exact test was only used to directly compare the two treatment groups, it takes no account of the controls. When the two sexes are analysed independently, it is found that in the group of females the significance of the relationship between the experimental manipulation and survival is improved (Fisher exact two-tailed probability = 0.029). In the group of males there is no significant relationship (Fisher exact two-tailed probability = 0.633), see Table 5.1 and Figure 5.1. In both sexes there is at least a trend for higher mortality with increased reproductive effort. The control groups demonstrate that the overwinter proportionate survival of both sexes in the experimental period is 0.56 (19 of 34 females, 26 of 46 males). In the group of individuals whose broods were enlarged, proportionate survival fell to 0.16 in females and 0.25 in males.

Table 5.1 The data set, illustrating the number of observations in each experimental category with the actual number of individuals alive and dead at the start of the following breeding season.

	Females			**Males**		
	Reduced	Enlarged	Control	Reduced	Enlarged	Control
Alive	6	1	19	5	2	26
Dead	1	5	15	6	6	20

Figure 5.1 The survival rates (proportion of all of the experimental individuals who were alive at start of the 1996 breeding season) of the different experimental groups in both a) males and b) females. Numbers beneath coloumns refer to sample size.

a)
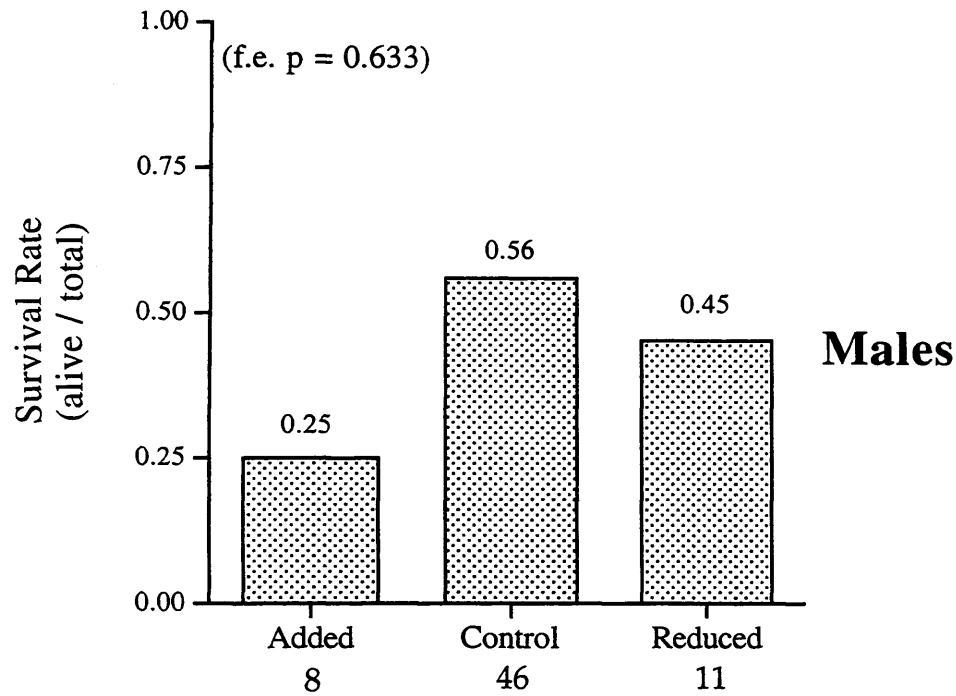
b)
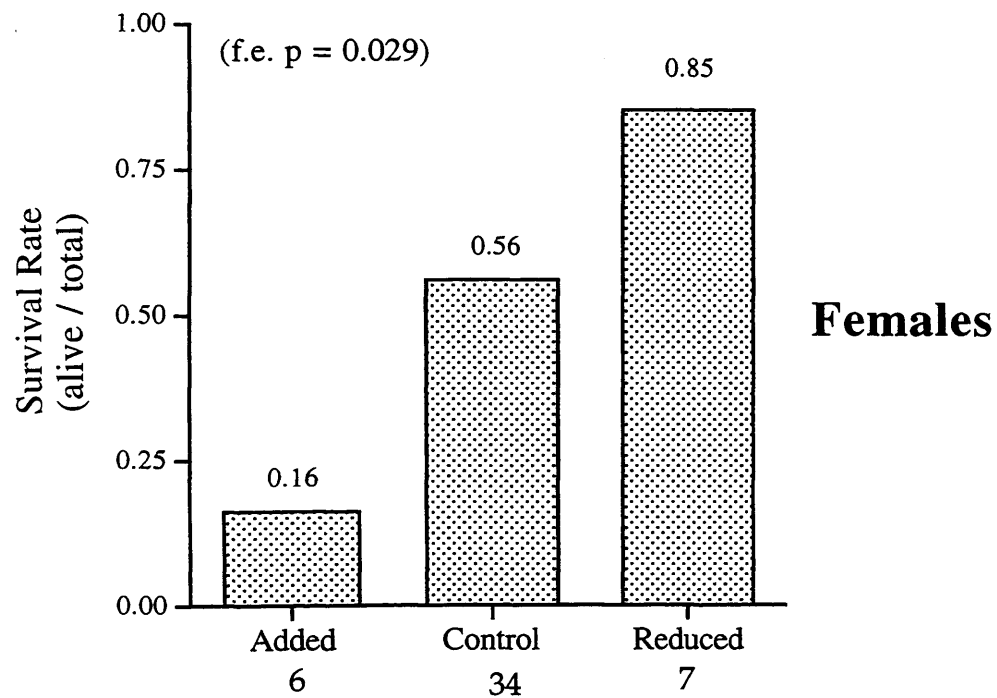
5.5 Discussion

We found a relationship between increased reproductive effort and a higher level of mortality. Whilst only a trend in males, it is highly significant in females. From this result, we would predict that these individuals with their current circumstances would pay a survival cost if they were to attempt to rear more young than they naturally had. Our result clearly supports the 'cost hypothesis' (Williams 1966; Morris 1992) which predicts that current reproduction is costly in terms of its effect on future survival - and thereby its effect on future reproduction.

Additionally, we have demonstrated that the cost of increased current reproduction is not shared equally between the sexes, there being a far larger cost revealed in females. This probably reflects a fundamental sex difference in this species, with females facing greater pressure to optimise their clutch size. If they overestimate the number of offspring they can 'afford' to rear they will suffer a cost to future reproduction.

There are, of course other ways in which this result could be interpreted. It is possible that selective pressures on males and females may be different with each sex operating under a distinct life history. For example, females may 'live fast, die young' which would mean that they would show an effect of the experiment sooner than males. Another problem that has been discussed in other similar work has been that of differential dispersal of the two sexes. In our isolated population this is very unlikely to have occurred.

There have been many other attempts to test the 'cost hypothesis' with eleven other studies in birds fulfilling the necessary condition of experimental manipulation of brood size (Table 5.2). It has to be appreciated that the majority of these other studies set out to test a variety of the trade-off hypotheses and the rigour with which the mortality estimates were made was not consistent across all studies. Perhaps of particular interest is the finding, in two studies of the same species (the blue tit, *Parus caeruleus*), of a complete reversal of sex-specific costs. In Nur (1988) female survival was reported to be linked to reproductive effort although there were year by year differences in the extent to which this cost was displayed. In Pettifor (1993) who worked on the same population, but used a different analytical approach, there was no relationship between female reproductive effort and survival but instead a significant relationship in the male. Against this, Pettifor (1993) suggests that

both of these results in the blue tit may be unsound, the results caused by inappropriate statistical analysis or sample size. In their study of the house sparrow, Hegner & Wingfield (1987) found no effect of brood size manipulation on mortality in either sex, however this result may be caused by very small sample sizes in some of their treatment groups. Alternatively, the duplicate studies of the blue tit and the house sparrow can be viewed as a demonstration that the mortality costs will vary both between different populations of the same species and temporally within the same population.

Table 5.2 Summary of the effect of brood enlargement experiments in altricial birds on the subsequent survival of parents. Negative, and zero effects are indicated by - and 0, respectively. # Denotes a part of a study in which the effect of a manipulation was not tested.

Species	Male	Female	Study
Pied Flycatcher (*Ficedula hypoleuca*)	-	#	Askenmo 1979
Tree Swallow (*Iridoprocne bicolor*)	#	0	de Steven 1980
Rook (*Corvus frugilegus*)	0	0	Røskaft 1985
Canada Goose (*Branta canadensis*)	0	0	Lessells 1986
Glaucous-winged gull (*Larus glaucescens*)	-	-	Reid 1987
Great tit (*Parus major*)	0	0	Pettifor et al. 1988
Collared Flycatcher (*Ficedula albicollis*)	0	0	Gustafsson & Sutherland 1988
Blue tit (*Parus caeruleus*)	0	-	Nur 1988
Blue tit (*Parus caeruleus*)	- *	0	Pettifor 1993
Kestrel (*Falco tunninculus*)	-	-	Daan et al. 1996
House sparrow (*Passer domesticus*)	0	0	Hegner & Wingfield 1987
House Sparrow (*Passer domesticus*)	0	-	This study

* This result believed to be inconclusive, see discussion in text.

Whilst it is interesting to observe the extent of variation (even within this limited sample [Table 5.2]), in the costs of reproduction in different species, of more interest to this particular study, and that of sexual selection itself, is the observed variation in the expression of a mortality cost of reproduction in the different sexes. Some of the studies found no mortality cost of an enlarged

brood, several studies found a cost borne primarily by one sex and two studies find an equal cost in males and females.

5.5.1 The cause and implications of sex-specific costs of reproduction?

In a socially monogamous species reproductive effort may differ between each sex as predicted by Trivers (1972). The female ultimately determines clutch size after a consideration of some, or all of the following (and others), physiological condition (Monaghan et al. 1995), mate quality (Burley 1986; Petrie & Williams 1993), costs of incubation (Moreno & Carlson 1989), and her perception of the amount of help or resources she may expect to receive from her partner (Högstedt 1980; and see Chapter Three). We assume that a female will normally lay the size of clutch that she, with her partner, is capable of rearing. By artificially increasing brood size we are potentially creating an unnatural dilemma for the pair. Due to the constraints of time, energy, and natural life expectancy we would predict that a female will increase her investment in the brood in proportion to the manipulation, in an effort to successfully fledge them. The male approaches the same dilemma in a different way and will respond according to several factors:-

i) amount of investment already made to the brood.
ii) his certainty of paternity (Whittingham et al. 1993).
iii) the opportunities for divorce and repairing, or polygyny (Veiga 1990).
iv) the opportunities for increased investment in alternative mating strategies for example the seeking of extra-pair paternity (Trivers 1972; Birkhead & Møller 1992).

Furthermore, over exertion by a male may lead to a) a reduced probability of survival to the next year (Reid 1987; Pettifor 1993; Daan et al 1990), or b) reduced future fecundity as a direct result of a decrease in the size of a condition-dependent sexual ornament (Gustaffson et al 1995) which may lead to reduced attractiveness and therefore fecundity. In a species in which males but not females display obvious condition-dependent sexual characters this type of trade-off will obviously only affect males.

The extent to which a male might be prepared to pay a survival cost for increased reproductive effort will be dependent on the other reproductive options which are available (i.e. extra-pair paternity), these will undoubtedly vary between species and populations (Birkhead & Møller 1992). Compared to

a female, a male will have more viable alternatives to feeding extra chicks (as under this manipulation). We would not necessarily expect a male to over-exert himself on an artificially manipulated clutch at the expense of other reproductive opportunities i.e. males may not be prepared to trade-off future reproduction for their present reproductive attempt.

Due to a lack of alternative reproductive options a female will have to adopt a 'best of a bad job' strategy and increase her effort at the current nest, this is a likely cause of the observed difference between the sexes in mortality. This result will support the prediction that females lay a smaller clutch than the one which will produce the greatest number of recruits (Lack 1954). Too large a clutch and the cost might be paid in lower overwinter survival, a smaller clutch may enhance her survival but also risk a non-adaptive lowering of reproductive output, particularly given that over-winter adult mortality runs at about 50% in this species and most females only get one chance.

CHAPTER SIX

Do large-badged house sparrows have enhanced over-winter survival?

6.1 Abstract

6.2 Introduction

6.3 Methods

6.4 Results and discussion

CHAPTER SIX

Do large-badged house sparrows have enhanced over-winter survival?

6.1 Abstract

The maintenance of variation in the expression of a sexual ornaments is often explained by a trade-off between fecundity and survival. At one end of the observed trait variation, individuals will not survive long but will enjoy high reproductive success, at the other, annual reproduction will be low but high survival will lead to multiple breeding opportunities. Effectively, the trade-off is sexual selection counterbalanced with natural selection (often through predation). Individuals advantaged by one will be disadvantaged by the other. Normally, it is expected that ornament size will be positively related to fecundity and negatively related to survival. Previously (Chapter Four), it has been demonstrated that badge size in the house sparrow is negatively related to fecundity, here we establish that it is positively related to survival.

6.2 Introduction

The reason that led Darwin to consider and propose the process of sexual selection (Darwin 1871) was that extravagant sexual ornaments appeared to be 'costly', in terms of reducing the survival prospects of the bearer. Such traits could not be explained by selection for adaptations that increased survival (Darwin 1859), and indeed this was used against him by the critics of natural selection. The 'costliness' of sexual ornaments is still a central tenet of sexual selection theory - the idea that for a signal to be honest it must be disproportionately costly to poor quality individuals is the crux of the handicap principle (Zahavi 1975, 1977; Grafen 1990a, 1990b; Pomiankowski 1987). The handicap principle can be viewed as a trade-off between the cost and benefit of producing and/or maintaining a given signal. Theoretically, such a trade-off is capable of sustaining the observed variation in sexual traits, and indeed there is some empirical support, particularly in cases in which the extravagance of the sexual ornament has been manipulated experimentally to

control for individual variation in access to resources. For example, in the barn swallow it has been demonstrated that an experimental elongation of tail length (a sexually selected trait), leads to increased mortality and decreased reproductive success (Møller 1989a).

In the house sparrow, *Passer domesticus*, Møller (1987; 1988; 1989b) found that those males with large badges (the black throat patch), were more successful in all measured aspects of both intra- and inter-sexual selection, for example social dominance and reproductive success. In further work he provided some evidence that this sexual selection is countered by natural selection, due to an increased level of predation by the sparrowhawk, *Accipiter nisus*, on those males with large badges, although the sample size was small. He concluded that "directional natural selection on badge size due to autumn mortality caused by predation maintains a stable badge size" (Møller 1989b).

In the study reported here, we tested the hypothesis that males with more pronounced badges are subject to stronger negative directional selection due to increased overwinter mortality. The study was carried out on a relatively closed island population so that survival of individuals could be monitored accurately.

6.3 Methods

The population of house sparrows studied was on Lundy Island, which lies in the Bristol Channel and is 20 km from the nearest mainland (English) coast. This isolated population is ideal for studying individual survival due to very low levels of immigration and emigration. Records from the bird observatory on Lundy in the 1950's and 1960's, when there were no resident sparrows present on the island, suggest a very low level of immigration (less than two individuals every three years)(Journals of the Lundy Field Society 1947-1997). There is no reason to believe that this level has increased, particularly as the population on the mainland has declined in recent years (Glue 1994). Also, despite many years ringing on Lundy, no island-ringed bird has ever been relocated on the mainland (British Trust for Ornithology pers. comm.). We can assume, therefore, that individuals which disappear from the population have indeed died.

The sexually dimorphic black throat patch of the male house sparrow is produced once a year during the annual moult in late summer (Summers-

Smith 1963). The feathers which make up the badge are black from the base with a 'buff tip' when first produced. Initially these buff tips conceal the blacker regions of the feathers and the full extent of the throat patch is concealed throughout the winter and into the spring. As the tips wear off, the badge becomes more visible, but its size will always be dependent upon the 'hidden' area from which the black feathers grow (Møller 1987, 1988; Veiga 1993, 1996). (For details of the badge size measuring protocol see section 3.3.2).

Between March-July 1995 all males on the island were captured, banded and measured. To enable visual recognition, all individuals were ringed with a unique combination of colour-bands and a metal ring supplied by the British Trust for Ornithology. Throughout the remainder of 1995 and 1996 survival was monitored by conducting extensive visual surveys at areas commonly frequented by the whole population (e.g. feeding areas, dust baths, roost sites). All extant individuals were recorded on multiple occasions during each survey, indicating that coverage of the whole population was complete. Individuals not sighted during a survey were adjudged to have died; this pronouncement was valid because individuals not recorded in a particular survey were never resighted thereafter. In each survey, all extant individuals were seen on multiple occasions and hence coverage of the whole population appeared to be sufficient. In July 1995 there were 46 males present in the population; of these, 21 (46%) were still present at the begining of the 1996 breeding season. We used the t-test to compare the badge sizes of birds that did survive the winter of 1995/96 with those that did not. A significant difference between these groups would suggest non-random mortality and possible selection.

Potential predators of the study population include the domestic cat (*Felis domesticus*), the European kestrel (*Falco tinnunculus*) and the sparrowhawk.

6.4 Results and Discussion

The 1995 summer badge sizes of the group of birds which survived the winter of 1995/1996 were significantly larger than those of the birds which died (Figure 6.1). Large-badged males appeared to survive better than small-badged males. This result does not support the hypothesis that showy, large-badged males suffer greater predation or selection than their smaller-badged counterparts (Møller 1989). In fact, it seems that counter to the finding of Møller (1989), those male sparrows with the largest badges actually survived significantly better than those with smaller badges. However, without performing an experimental manipulation of badge size to control for other differences between individuals (Lessels 1986; Reznick 1990), it is difficult to speculate on the causes of this apparent selection. This result is unlikely to be affected by the brood manipulation experiment reported in Chapter 5 because in that experiment the manipulation was found to be independent of badge size ($r^2 = 0.009$, n = 46, p > 0.5).

Figure 6.1 The summer 1995 badge length (mm) of males, grouped as being dead or alive in the spring of 1996. (error bars indicate ± standard error). Alive: mean = 34.99, n = 21, s.d. = 4.00. Dead: mean = 31.52, n = 25, s.d. = 4.80. Difference between the two groups given by two-tailed unpaired t-test, p = 0.012.
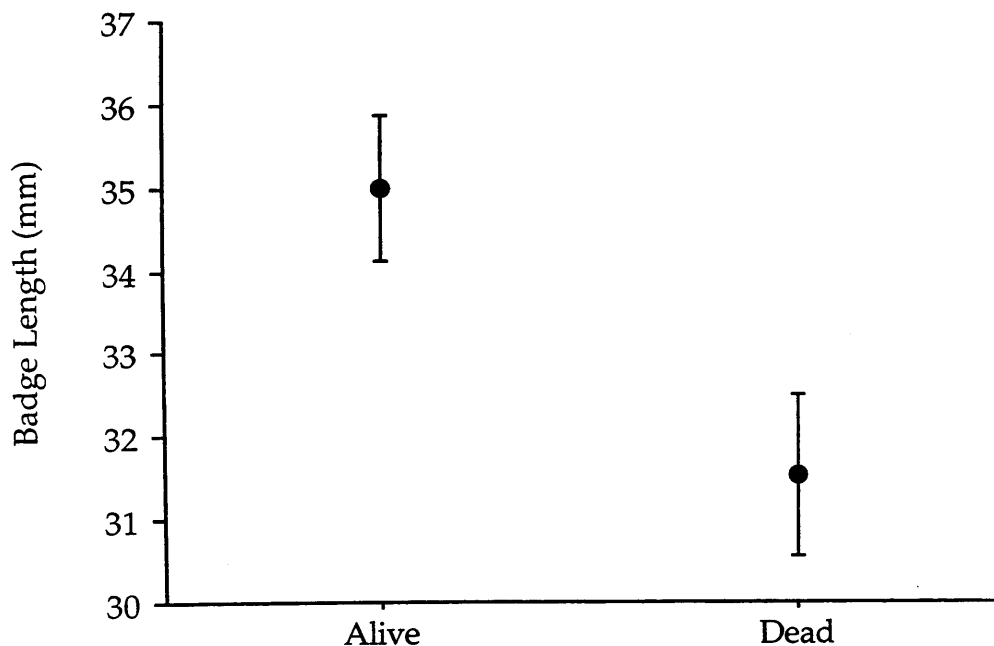
What is the empirical evidence that showy males do pay a cost through increased mortality? In birds, there have been several attempts to prove that a trade-off between showy plumage and mortality exists. Promislow et al. (1992) used a comparative analysis to test for a relationship between male brightness and male mortality across many different species. They found a positive relationship between male brightness and mortality but this was between species not within a single species (but see Owens & Bennett 1994).

In other taxa there is some evidence that certain sexual signals carry an increased risk of predation (e.g. in guppies *Poecilia reticulata*, Endler 1988; sticklebacks, *Gasterosteus aculeatus* Moodie (1972); and invertebrates and lower vertebrates as reviewed in Magnhagen (1991)). Despite this evidence, there is no reason to suppose that avian plumage traits will operate in the same way as for example an acoustic frog call. Additionally, many models of sexual selection have been proposed which do not require showy traits to carry a mortality cost (Andersson 1982, 1986; Price et al. 1993; Schluter et al. 1991). Indeed, at least three models predict that the showiest males will have increased viability (Baker & Parker 1979; Nur & Hasson 1984; Zeh & Zeh 1988).

In birds, most of the experimental work has focused on the testing of the 'unprofitable prey hypothesis' (Baker & Parker 1979), which proposes that brightly coloured individuals signal to predators that they will be hard to catch. This model was originally stimulated by the lack of evidence in support of the sexual selection theory which invokes a predation cost for showy plumage. There is some good support for the alternative unprofitable prey model, provided in particular by the work of Götmark (1992, 1993, 1995) who studied experimentally the response of predators to manipulated models of prey species, so removing the potentially confounding effects of correlations between plumage traits and resources or general viability. In one of these studies, Götmark (1994) also demonstrated that a novel plumage character does not lead to elevated predation.

Although the unprofitable prey model may be useful in accounting for the initial evolution of a plumage trait, it will not explain the observed high variation in sexual plumage traits. However, Götmark's results are entirely consistent with two other sexual selection models which predict a positive relationship between a sexual trait and an increased viability (Zeh and Zeh 1988; Nur and Hasson 1984). Both these models are based on the idea that many sexual signals will have a high phenotypic plasticity and will therefore be condition-dependent. Those individuals in superior condition will be able

to produce the most showy trait and also have a higher survival. This may occur in a system with or without a significant predation rate on adults: viability may be dependent on numerous other variables such as pathogens, weather conditions and food abundance. If predators are active in a population, then presumably if they can detect a trait it would be adaptive for them to tune into its signal and save their energy by not chasing those individuals in the best condition. The subtle difference between this and the unprofitable prey model is that in this case, the signal is predominantly aimed at conspecific females, not the predator. This does not preclude the predator from being just as good as a female at interpretating the signal.

There are already two empirical examples of sexual traits which, consistent with the result reported here, support the two models given above. These two unmanipulative studies demonstrate preferential survival of those males with the showiest sexual ornaments. In the house finch *Carpodacus mexicanus* and the peacock *Pavo cristatus*, individuals with the most colourful plumage and the longest trains, respectively, were shown to be more viable than less well endowed males (Hill 1991; Petrie 1992, 1994). The conclusion of these studies is that the most showy males either had access to the best resources and/or had better genes than other males. Whilst predation may account for the mortality in these studies, it is generally accepted that the likelihood of being predated will relate to general condition. Hence, although the observed relationship between trait expression and viability is mediated by predation it is likely that it is not predation *per se* causing the relationship, but rather, that high quality males exhibit both large or colourful traits and high survival.

The badges-of-status model proposed by Rohwer (1975) to explain plumage variation in the Harris sparrow, *Zonotrichia querula*, makes predictions consistent with the result reported here. In the Harris sparrow (actually not a true sparrow but a bunting, a member of the *Emberizidae*) winter flocks are formed and a plumage trait very similar to that found in the house sparrow is used to signal dominance. Within the flock, males with large badges are dominant over individuals with smaller ones. It seems likely that in a competition for resources (e.g. the best roost sites and food) large badged males will prevail and therefore increase their chances of overwinter survival. The badges-of-status hypothesis has previously been examined in the house sparrow by Veiga (1995) who used a badge size manipulation to study the costs of cheating. Males that had their natural badges enlarged did indeed suffer higher mortality, particularly the younger ones. The result of Veiga's study is

of great importance, because by randomly assigning males to different treatment groups he achieved a disassociation of badge size and the phenotypic variables that might otherwise have confounded his result. One of the acknowledged problems of Veiga's study is that his population is not enclosed and it is possible, though perhaps unlikely, that the result may have been due to dispersal. Due to the closed nature of our population we can exclude the possibility of dispersal as the cause of our result. Together with our result, Veiga's study enables us to reject Møller's (1989) hypothesis that males with the largest badges suffer increased predation.

If large-badged male sparrows do not suffer higher mortality then we are left with the problem that caused Møller to propose the idea in the first place: if large-badged males survive better and have a reproductive advantage, then why does variation still exist and why has the badge not become fixed at a still greater size? There are several possibilities that could be used to explain this apparent paradox. Either (i) the badge is currently in transition, increasing progressively in size; (ii) it is not, as is commonly assumed, attractive to females, if for example there is a trade-off between viability and fecundity (Schluter et al. 1991); or (iii) the badge is non-heritable and therefore cannot progress to fixation. It has been predicted (Zeh & Zeh 1988; Nur & Hasson 1984) that if variation in a sexual trait has a high environmental component, then highly ornamented males may survive better than those with smaller ornaments.

We have demonstrated that in our population, large badge size in the male sparrow does not carry a cost of higher mortality. In order to further investigate the causes of continued variation in this trait it will be necessary to examine the underlying determinants of badge size. Is the variation in badge size caused by condition-dependence or is it maintained by a high level of additive genetic variation?

CHAPTER SEVEN

Non-genetic "inheritance" of a sexually selected trait.

7.1 Abstract

7.2 Introduction

7.3 Methods

7.4 Results

7.5 Discussion

CHAPTER SEVEN

Non-genetic "inheritance" of a sexually selected trait.

7.1 Abstract

Through a cross-fostering study of a population of house sparrows in the field we examined the heritability of a sexual ornament, the black throat patch of the male. Here we demonstrate that observed variation in the expression of this sexually selected trait has an environmental component with no evidence for additive genetic variation. The implications of this lack of genetic heritability and consequent condition-dependence, to sexual selection theory are discussed. Whilst we find no direct support for 'good genes' hypotheses, handicap models which stipulate condition-dependence for sexual ornaments will be favoured.

7.2 Introduction

The black throat patch (or 'badge' : Dawkins & Krebs 1978) of the male house sparrow has been shown to be a sexually selected trait with a female preference for large-badged males (Møller 1988, 1989). The maintenance of both the female preference, and the male trait itself, will depend on the signal conveying information to the female that is actually useful and reliable. Therefore the signal must be honest and a mechanism to prevent cheating must be in operation (Zahavi 1975, 1977; Grafen 1990a, 1990b). Females choosing large-badged males should ultimately gain either direct- (Heywood 1989; Hoelzer 1989; Kirkpatrick & Ryan 1991), or indirect benefits (Williams 1966; Hamilton & Zuk 1982) i.e. benefits for her own fecundity or for the benefit of her offspring respectively.

Previous work with this population of house sparrows has shown that contrary to the 'good parenting' hypothesis, large-badged males contribute less to provisioning of young than their small-badged counterparts (Chapter Three). It has also been revealed that counter to expectations from the direct

benefit models, large-badged males - and the females paired with them - have a lower annual reproductive success than smaller-badged males (Chapter Four).

The failure of the 'direct benefits' models to explain the female preference for large-badged males in the Lundy population leaves two possibilities to explain the variation in badge size. Firstly, there may not be an adaptive reason for the current maintenance of variation in badge size. For example, even if the variation in badge size was associated with variance in reproductive success at some point in history, there is no reason why it has to be now; there are other mechanisms available that are capable of maintaining the observed variation (Grafen 1988). Secondly, mate choice by females may be driven by them seeking 'good genes' for their offspring (Williams 1966, Lande 1981; Hamilton & Zuk 1982; Petrie 1994). If females do use badge size to select for good genes, and they prefer large-badged males, then it follows that the genes of these males must be preferable in some respect. Good genes are predicted to confer either general viability (e.g. Hamilton & Zuk 1982), or attractiveness on their bearer (Fisher 1930).

It is normally assumed that for a good genes explanation to account for ornament size there should be a discernible genetic component to the trait, an assumption for which in birds there is limited empirical support (Grant 1990; Norris 1993; Andersson 1994). Fisher's fundamental theorem predicts that, because, all other things being equal, natural selection must erode the extent of additive genetic variation, there should be little genetic variation in those traits closely correlated with fitness - hence, after some time, natural selection should cease to act on such traits (Fisher 1930). This leads to the Lek paradox (Reynolds & Gross 1990; Kirkpatrick & Ryan 1991); in those lekking species (and some others), in which females get nothing from males but sperm, female choice will be very strong, and according to Fisher's fundamental theorem additive genetic variation quickly exhausted. However, these are exactly the circumstances where 'good genes' processes are usually invoked. Why would females show strong discrimination for males in lekking species when there is predicted to be a minimal potential gain, with very low additive genetic variation for sexual traits amongst the males? Several attempts have been made to tackle this problem. Charlesworth (1987) showed that mutation could potentially drive the variation in traits and female choice. Reynolds & Gross (1990) and Kirkpatrick & Ryan (1991) argued that females must be gaining some direct material benefits. Most recently Pomiankowski & Møller (1995) attempted to resolve the lek paradox by tackling Fisher's fundamental

theorem. They proposed a genetic model which would ensure and enhance genetic variability for sexual traits.

An alternative way of resolving the lek paradox would be a demonstration that it does not in fact exist, i.e. if, in fact, sexual ornaments are not genetically heritable (Rowe & Houle 1996). There are several models which predict a low genetic inheritance of sexual ornaments (Nur & Hasson 1984, Zeh & Zeh 1988, Wolf et al. 1997) and high condition-dependence. There is theoretical support for this idea (Price et al. 1993; Andersson 1994; Johnstone 1995) but as yet very little empirical evidence. If this conjecture is true and traits exhibit a high degree of phenotypic plasticity, then any observed genetic component may be caused by covariation with genes for viability. The extent to which this genetic component is revealed will be entirely dependent on any viability pressures the population faces.

Møller (1989) observed a significant similarity between badge size values from fathers and their sons. This was interpreted as being due to additive genetic variation, although Møller did not control for the shared common environment between a male and his sons. Separating genetic and environmental components is essential to a thorough examination of true genetic heritability and can be achieved in the field by using cross-fostering (Smith & Dhondt 1980). Cross-fostering of broods of chicks between nests will ensure that offspring are not reared by their genetic father, thereby disassociating genetic causes of trait expression from environmental ones, although there may still be some maternal effects operating by investment in the egg and incubation. Regressing trait expression in parents and offspring will reveal underlying environmental (foster father) and genetic (genetic father), causes of variation in trait expression (Falconer 1960).

The main aim of this work was to examine the heritability of badge size as reported by Møller (1989). Was the reported relationship between father and offspring due to genetic or environmental effects? We have used a cross-fostering approach to reveal the genetic and environmental component of the house sparrow's badge. To achieve the main aim it was necessary to cross-foster as many offspring as possible for two reasons. Firstly, badge size is only expressed about three months after fledging, by which time there will have been substantial mortality of offspring; secondly, of course, it is only expressed in male offspring which will halve the sample size.

Finally, it is important to ensure through genetic paternity analysis that the putative genetic father is the actual genetic father. The occurrence of extra-pair paternity may lead to multiple paternity within a single brood. Mismatching offspring with the wrong genetic parent will inevitably lead to error (Sheldon et al. 1997).

7.3 Methods

7.3.1 The study population

This study was carried out between January 1995 and October 1996 on Lundy Island, 20 km off the south west coast of England (51'11" N 4'40" W). For further details of the study site see Chapter Two. The population is very sedentary and lives within a small area (less than 1 km²) which enables easy retrapping of all adults and juveniles for the measurement of badge size. All individuals in the population were caught using mist nets, walk-in and nestbox traps, and were ringed with metal BTO rings and individual combinations of colour-bands for identification in the field.

7.3.2 Measuring the badge

The black throat patch of the adult male house sparrow is produced once a year during the moult in late summer. Juvenile males fledge in a monomorphic dull plumage and produce their first badge in the autumn (about three months after fledging); subsequently, the plumage of yearlings and adult males is identical. At the time of moult, the feathers which make up the badge are mainly black but have a pale buff tip. Initially, these buff tips hide the blacker regions of the feathers and the full extent of the throat patch is concealed throughout the winter and into the spring. As the tips wear off, the badge becomes more visible, but its visible size will always be dependent upon the extent to which the buff tips have worn away (Møller 1987; Veiga 1996). To obtain a repeatable measure of 'badge size' throughout the year, the length was taken with callipers from the base of the bird's bill to the posterior limit of the badge at the base of the feathers. This measurement is highly repeatable throughout the whole year, not just when the buff tips have worn off ($r = 0.76$, $F_{12,13} = 7.78$, $p < 0.001$; calculated after Falconer (1960)). Importantly, this 'hidden' length is highly correlated with the length of the visible badge ($r^2 = 0.47$, $n = 47$, $p < 0.001$).

7.3.3 The cross-fostering experiment

All breeding attempts were in artificial nest boxes which were closely monitored to allow prediction of the hatching date from the date of clutch completion. Two broods were only cross-fostered if they hatched in the same 24-hour period, largely as a precaution against parental desertion. Whole broods were swapped with each other as opposed to the alternative approach of partial cross-fostering, which might potentially produce unnaturally asynchronous broods. Most house sparrow broods are asynchronous with chicks hatching at different times, and being of various sizes, there is some evidence that this is adaptive (Veiga & Vinuela 1993), and disrupting this pattern might therefore lead to a bias of the results. Where possible, broods of similar size were swapped. In 1995, following the above criteria, 80% (44/55) of broods, containing a total of 139 individual chicks, were cross-fostered. The results of this study are not confounded by extra-pair paternity as there were no extra-pair offspring in the sample (Chapter Two). The cross-fostering was done randomly with respect to adult male badge size and there was no relationship between the badge size of genetic father and foster father ($r2 <$ 0.001, n = 33, p > 0.9).

All chicks reared in the population in 1995 were ringed and colour-banded in the nest. During October 1995 and January 1996, all birds in the population were retrapped and morphological traits were measured.

7.3.4 The measurement of heritability

To measure the genetic component of variation in badge size we took the badge size of the male at the time of chick rearing (summer 1995) and the size of the badge produced by the offspring in their first moult (winter 1995/96). In most cases each male had only one surviving male offspring. However, in those cases where more than one survived it is standard to take the mean badge size of the offspring (Falconer 1960).

Our estimate of the heritability (h^2) of badge size was taken to be twice the slope of the linear regression between the badge size of the father and mean badge size of all surviving male offspring, based on the assumption that the character is inherited equally from the father and the mother (even though it is not expressed in females)(Falconer 1960).

Data were tested for departures from normality using the Lilliefors test (Wilkinson 1992). Residuals of regressions were also checked for normality; in both cases a probability of $\leq$ 0.05 was taken to indicate biological significance. Linear regressions were carried out using SYSTAT Version 5.2 (SYSTAT, Evanston, IL., USA).

7.4 Results

In the group of cross-fostered offspring there was no relationship between the length of a male sparrow's throat patch and the length of his genetic father's throat patch, suggesting that in this population there is no discernible additive genetic component to badge size ($h^2 < 0.001$, p > 0.5)(Figure 7.1a). However, a highly significant positive correlation between the length of an offspring's throat patch and that of his foster father (r = 0.616, p = 0.005)(Figure 7.1b) was observed, indicating that there is a substantial environmentally determined component for variation in this trait. The sample size (18 or 19) is much lower than the number of broods swapped (44) due to the natural level of offspring mortality between the breeding season and the recapture of offspring in the autumn (after the badge was produced).

Table 7.1 Heritability estimates for badge length between mean male offspring and their genetic and foster fathers.

	h^2	S.E.	r	n	p
Genetic father	0.006	0.150	0.004	18	0.985
Foster father	0.792	0.123	0.616	19	0.005

Figure 7.1 Linear regression of mean offspring badge length in **a)** 18 cross-fostered broods on that of their genetic fathers and **b)** 19 cross-fostered broods on that of their foster fathers

a)

Genetic father badge length (mm)

$r^2 < 0.001$
$n = 18$
$p > 0.5$

b)

$y = 0.396x + 18.764$

$r^2 = 0.380$
$n = 19$
$p = 0.005$

Foster father badge length (mm)
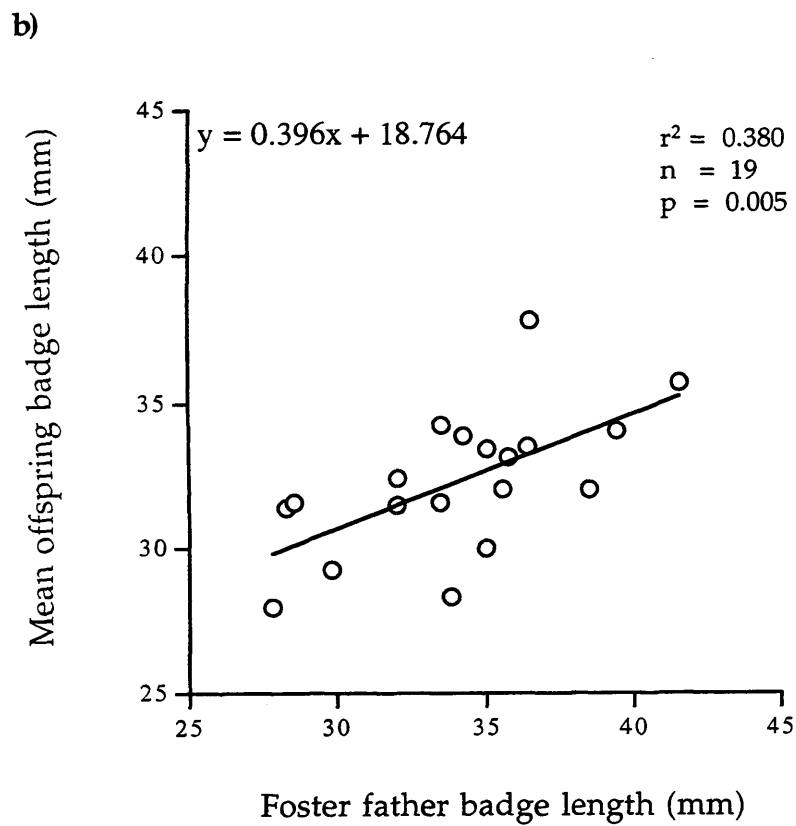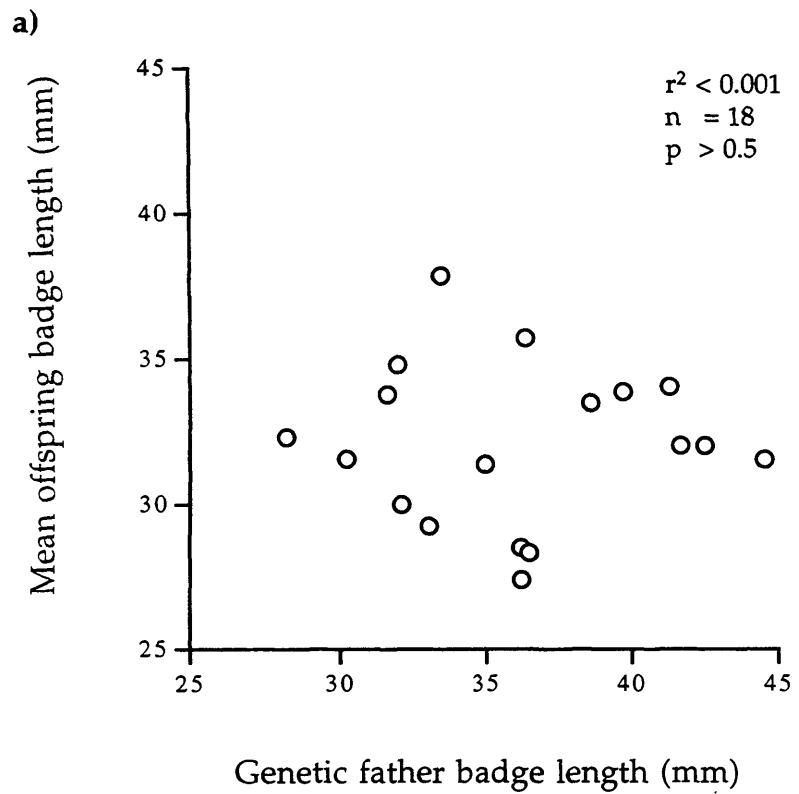
7.5 Discussion

We found strong evidence for non-genetic determination of variation in badge size in the house sparrows on Lundy but no evidence of additive genetic variation and therefore heritability. Our results are consistent with the finding by Møller (1989) of a relationship between the badge size of a male sparrow and the badge size of his sons. However, whilst Møller ascribed this heritability of badge size to additive genetic variation, we have demonstrated that, on the contrary, there appears to be a large environmental component.

It is well known, of course, that information may be passed from generation to generation, with many classic examples of sexual imprinting (reviewed in Bateson 1978) and even the environmental transmission of a secondary sexual trait (bird song), with young male zebra finches (*Poephilia guttata*) learning their song from the male who rears them (Immelmann 1969). There is also widely acknowledged evidence that morphological phenotypic traits have a substantial environmental component, e.g. the effect of temperature and season on development in young red deer, *Cervus elaphus* (Clutton-Brock 1988) and birds (Boag 1987). Also a study by James (1983), revealed a significant environmental component to the morphology of the red-winged blackbird *Agelaius phoeniceus* using cross-fostering between populations exhibiting different clines of character variation. Despite this widespread evidence for strong environmental components on general morphological and behavioural traits to our knowledge this is the first evidence for the environmental determination (at the rearing stage) of a sexually selected ornament; despite the prediction that some sexual ornaments should be more sensitive to environmental determination than morphological traits (Nur & Hasson 1984; Zeh & Zeh 1988; Wolf et al. 1997). Condition-dependence is one mechanism given for the maintenance of a reliable signal (Veiga 1993; Owens & Hartley 1998). Both nutritional constraints (Hill & Montgomerie 1994) and pathogens (reviewed in Clayton 1991) have been shown to affect condition-dependent traits. Indeed, the badge of the house sparrow has been shown to be partially determined by nutritional constraints (Veiga & Puerta 1996).

If the badge is phenotypically plastic, then the existence of a relationship between the badge size of a male and his son is not too surprising, with several possible explanations. Firstly, the badge size of a male may signal some form of direct benefit that will benefit the offspring. For example, if badge size is determined by nutritional constraints then perhaps the nutritional environment in which a chick is reared will have some effect on the size of its

badge. Whilst this is a possibility; we have previously demonstrated that chick-feeding by males is dependent upon badge size; (Chapter Three), the observed relationship with large-badged males feeding their chicks at a relatively low rate and the study of Veiga & Puerta (1996) would suggest that this would lead to small badge size in the offspring of large-badged males. Also, overall feeding by the pair is unrelated to the badge size of the male (Section 3.4.3).

Secondly, if parasites do affect the expression of badge size (Hamilton & Zuk 1982), then perhaps the parasite environment of the nest, or even direct parasite contagion between father and son (Hamilton 1990), may affect the expression of the trait.

Thirdly, and perhaps most intriguingly, if the badge of the house sparrow has a status-signalling role in male-male competition (i.e. a positive relationship between badge size and dominance), as suggested by Møller (1987a,b), one of several nepotistic mechanisms may account for the observed environmental component. During the period (about two weeks [Summers-Smith 1963]) in which males feed their fledglings out of the nest, a male with a large badge (presumably dominant), may protect his offspring from harassment by other males. Assuming that individuals within a small flock can recognise each other, then it is quite possible that other males will treat a young male in the same way as its father, for fear of retribution. In this way, a young male will assume the dominance of his father and gain a similar degree of access to resources, therefore producing a similarly sized condition-dependant badge. A more simple alternative is that males learn to recognise their (foster) sons during the period when they care for them and subsequently will favour them in dominance interactions within the flock. Many other mechanisms can be proposed in which a male could gain an advantage which is in proportion to his father's badge (and dominance), all of which could explain the observed relationship.

Regardless of the mechanism involved, the implications to sexual selection theory of a low genetic component for a sexually selected trait are profound. Firstly, the observed result will not support Fisher's theory of runaway selection (Fisher 1930) in which female preference for a male trait is genetically linked to trait expression genes. This theory initially relies on variation in the trait having a significant genetic component and will continue to rely on this for all the time that the trait is sexually selected.

At first sight, it might be expected that the group of theories, collectively known as the 'good genes' models, would not be supported by a lack of genetic inheritance for a sexual trait. In fact, it could be argued that many good genes models require a trait that has a high environmental component. A condition-dependent trait will inform others of the state of an individual in a given environment. Models of sexual selection which include indicator mechanisms (Zahavi 1975, 1977; Hamilton & Zuk 1982; Pomiankowski 1987a, b; Grafen 1990) call for a trait which is highly sensitive to a wide range of genotype/ environment interactions and hence presumably has a low direct genetic inheritance. A condition-dependent trait with a significant environmental component may provide an honest signal of genetically determined higher general viability. If this were true, we might still expect a relationship between character expression in males and their genetic offspring but only under conditions where there is a viability challenge. For example, in the given model of parasite mediated sexual selection, a condition-dependent trait may show a degree of variation in a population, even in the absence of parasites. The observed variation will be due to components of the environment and there will be no relationship between trait expression and parasite resistance genes. If this population of individuals is then challenged by the parasite, those individuals carrying the gene for resistance will be at an advantage phenotypically, and will subsequently produce a better condition-dependent trait. An observable relationship between trait expression and viability genes (for parasite resistance) will now exist and will appear to be directly genetically heritable, even though any inheritance will be indirect.

In conclusion, variation in size of the badge of the house sparrow has been demonstrated to have a significant environmental component. Although the precise mechanism for this determination is unknown, the observed relationship is useful in the consideration of rival theories of sexual selection. The model of Fisherian runaway selection will not be supported by the observed badge-determining mechanism. Alternatively, the demonstration of a high environmental component to badge size variation is highly favourable to those 'handicap' models which stipulate condition-dependence as a mechanism for maintaining the honesty of a sexual signal.

CHAPTER EIGHT

Discussion: female choice in the house sparrow

8.1 Abstract

8.2 The study

CHAPTER EIGHT

Discussion: female choice in the house sparrow

8.1 Abstract

We have assessed the benefits to females of expressing a preference for those males with large badges. We found no evidence for *direct benefits* with large-badged males contributing less effort to chick-feeding than their smaller badged counterparts. In overall annual fecundity females also seem to suffer a cost of pairing with large badged males. Large-badged pairs contribute less fledglings to the population of young sparrows and are also predicted to recruit significantly fewer offspring into the breeding population a year later. The female house sparrow alone appears to bear a significant cost of reproductive effort. This result, which perhaps points to a fundamental difference between the sexes in monogamous passerine birds may also explain why a female paired with a large-badged male lays a smaller clutch. To explain the apparent paradox of female choice leading to lower fecundity, indirect benefits were examined, primarily the heritability of the male badge. A substantial environmental component was revealed as the underlying cause of variation in this sexual ornament, with no observable additive genetic variation. This result supports the idea of the badge as a condition-dependent ornament. The natural relationship between male badge size and overwinter survival also supports this view and points to status-signalling between males as a likely mechanism for maintaining the honesty of the badge.

While most models of sexual selection assume that ornament size is positively related to fecundity and negatively related to survival it appears in our population of house sparrows that the opposite is true - badge size is negatively related to fecundity (lazy males) and positively related to survival.

8.2 The study

8.2.1 Low levels of EPP: is there an island effect?

The initial aim of this research was to study female choice of extra-pair males and the benefits of this choice to offspring. The unexpected finding of a very low level of extra-pair paternity had serious consequences for this initial aim but was of great interest in itself. Extra-pair paternity is very common amongst passerines (Owens & Hartley 1998) and previous studies in this species have revealed levels of extra-pair paternity (EPP) approaching 15% (Wetton & Parkin 1991; Kimball 1995; I. Stewart pers. comm.). Given the high nesting density of our colony, and the conclusion from previous studies that high nesting density enhances the likelihood of EPP, we expected the frequency of EPP to be at least this high. The finding of less than 1% EPP in our population in each of two years was initially surprising. Recent work by other groups suggests that this low level of EPP, whilst being at odds with that of other populations of the house sparrow, is consistent with the low level of EPP in small isolated populations of other species. A population of the silvereye (*Zosterops lateralis*), studied for many years on Heron Island, Queensland, Australia, was shown to exhibit no EPP (Robertson 1996)(although there is no contrasting mainland study to compare with this). A more pertinent and perhaps more striking example is that of the great tit (*Parus major*) population studied on the island of Vlieland in the Dutch Wadden Sea. In this population, EPP occurred at a frequency 3.5% (Verboven & Mateman 1997), which contrasts markedly with other EPP estimates in the same species (three estimates between 14% and 18% (referenced in Verboven & Mateman 1997). Verboven & Mateman suggest that result is due to the low breeding density of their population.

In a recent comparative analysis, Westneat and Sherman (1997) found support for the idea that within a species, the rate of EPP does increase with breeding density. However, further investigation into the levels of EPP in different great tit populations and nearest neighbour distances (the usual measure of breeding density in birds) reported in those populations provides (of course, it can't anyway with only three populations) no support for density as the underlying cause (Table 8.1).

Table 8.1 Frequency of EPP in different populations of the great tit and average nearest neighbour distances.

Population	Level of EPP	Ave. nearest neighbour (m)	Reference
Vlieland	3.5%	47.2 ±3.1 SE	Verboven & Mateman 1997
Uppsala	15.0%	97.0 ±35 SD	Gulberg et al. 1992
Wytham	14.0%	50	Blakey 1994

Although the comparison between the different studies may be crude in some respects, it seems unlikely that the low level of EPP on Vlieland is caused by the low breeding density as, in fact, this is the population with the highest breeding density of the three.

The published number of estimates of EPP in the house sparrow does not quite compare with that of the great tit; however, a number of unpublished reports allow us to make a crude comparison of inter-population EPP differences in this species (Table 8.2).

Table 8.2 Frequency of EPP in different populations of the house sparrow.

Population	Level of EPP	Ave. nearest neighbour (m)	Reference
Nottingham, UK	13.6%	5	Wetton & Parkin 1991
Lundy Island	0.9%	7	This thesis
Helgeland, Norway (archipelago)	4.7%	5	IRK Stewart pers comm
Kentucky, USA	10.5%	5	IRK Stewart pers comm
Albuquerque, USA	12.7%	Unknown	Kimball 1995

There may of course be many other reasons why levels of EPP differ between populations, none of which we can test with such a small data set. However, once again density does not seem to play a significant role in the determination of the EPP level. In the two very crude comparisons above, in both the great tit and the house sparrow the outlying groups with regards to the level of EPP are those populations isolated on islands. It has been

suggested that the cause of this low EPP may be low genetic diversity in these populations (Petrie & Kempenaers 1998). This idea is consistent with the finding that, comparatively, genetic diversity is lower in island populations (Frankham 1997). Although the latter study was a comparative work across all taxa, birds are included, and even alone they still exhibit significantly lower genetic diversity in island populations.

In conclusion, the observed low level of EPP in the study population of house sparrows may or may not be due to the effects of low genetic diversity caused by such factors as inbreeding or founder effects. A comparison of the genetic variability in this population with mainland populations would be a useful and interesting study. We have demonstrated that, within a species, levels of EPP can differ significantly. Further examination of the causes and effects of these different levels, both within and between populations, will serve to enhance our understanding of extra-pair mating and its importance to the process of sexual selection.

8.2.2 Within-pair mate choice

While the low level of EPP in the study population constrained the main objective of this study - female choice of extra-pair partners - it did allow a study of within-pair mate choice, unconfounded by the effects of EPP.

No attempt was made to study female preference for particular male phenotypes directly. Previous work by Møller (1988), Veiga (1993) and Wetton et al. (1995) led us to assume that female house sparrows did prefer those males with the largest badges. Møller (1988) used two approaches in his study of the attractiveness of male house sparrows. Firstly, he tested the response of females, which had been hormonally manipulated into breeding condition, to taxidermic mounts of male sparrows with different sized badges. It was found that females solicited more copulations from those models with the larger badges (Møller's experiment does not necessarily distinguish between pair- and extra-pair mate choice, as these females were all unmated). Secondly, in the wild it was discovered that male sparrows with a high mating success had bigger badges than those with a low mating success. Mating success was measured as the date of initiation of singing in the spring, the acquisition of a mate, and the establishment of a territory with multiple nest sites.

On the assumption that female sparrows do prefer those males with the largest badges, we set out to discover what benefits females can expect to gain

from such mate choice. To a large extent this was achieved through a correlative approach, looking for relationships between pair male badge size and direct and indirect benefits to females. In a monogamous avian mating system, there are many potential benefits available to females, (Table 3).

Table 3. Examples of direct and indirect benefits a monogamously paired female could expect from her pair male.

Benefit	Species	Reference
DIRECT		
Nest site	Pied flycatcher (*Ficedula hypoleuca*)	Alatalo et al. 1986
Territory	Pied flycatcher (*Ficedula hypoleuca*)	Alatalo et al. 1986
Courtship gifts	Common tern (*Sterna hirundo*)	Wiggins & Morris 1986
Incubation help	Moorhen (*Gallinula chloropus*)	Petrie 1983
Chick feeding help	House finch (*Carpodacus mexinus*)	Hill 1991
Nest defence	Dark-eyed junco (*Junco hyemalis*)	Enstrom et al. 1997
Increased fecundity	Barn swallow (*Hirundo rustica*)	Møller 1994
INDIRECT		
Genes for parasite resistance	Barn swallow (*Hirundo rustica*)	Møller 1990
Genes for ornament	Great tit (*Parus major*)	Norris 1993
Genes for offspring viability	Peacock (*Pavo christatus*) *	Petrie 1994

* does not a have monogamous mating system

With the exception of good genes benefits, all of the other benefits illustrated in Table 3 have been observed in birds paired monogamously. In different species, different benefits will be of lesser or greater importance and are not necessarily always applicable. In the population of house sparrows studied here, nest site will be relatively unimportant due to the homogeneity and excess of available artificial nest boxes. The house sparrow does not defend a territory and the male house sparrow does not contribute significantly to incubation (he does not have an incubation patch) and therefore any territorial, and incubation advantages to the female will be negligible. Likewise, there is no evidence of courtship feeding and, with a lack of nest predators on the island, little benefit from any nest defence from a male partner. It seems likely that the main potential benefits a female house sparrow can achieve from her mate are help with chick feeding, increased fecundity, and good genes.

8.2.3 The search for female benefits of mate choice

The most likely, and perhaps easiest to score female benefit is male help at the nest with chick feeding. One of the primary constraints that has led many birds (particularly small passerines) to develop monogamy as a mating system is the laying of eggs and rearing of altricial young. Leaving offspring in a nest will make them vulnerable to predation and the elements. The chances of rearing offspring to the relative safety of independence will be increased by biparental care (Lack 1968; Gowaty 1996). Additionally, the potential costs of deserting a brood (and mate) are often high in comparison to the potential benefits i.e. getting a new mate, it is probably the lack of benefits that stops passerines deserting their broods (Owens & Bennett 1997).

Male chick feeding is relatively easy to score through standard behavioural procedures and will presumably constitute a benefit to the female. The hypothesis to be tested was whether male badge size would be useful to a female to predict the level of male help she could expect. For example, in the house finch (a North American bunting), it has been found that the extent of red coloration of the male is an accurate predictor of the contribution of males to chick feeding (Hill 1991). If there were a relationship between badge size and direct benefits (chick feeding help), then the relationship was expected to be positive.

Surprisingly, it was discovered in this population that although badge size does correlate with the relative contribution to chick feeding, the relationship was negative. Males with the smallest badges actually provided relatively more help with chick rearing (assuming that load sizes between males of different badge size are equal). Females therefore gained no direct chick feeding benefits by choosing males with large badges.

Despite the lack of chick feeding benefits, females might still benefit overall from pairing with a large-badged male if that increased their fecundity and hence reproductive success. In birds, as in most higher organisms, the production of offspring is largely controlled by the female, both in terms of timing, and output. There is much debate about the optimum clutch size of individuals/ pairs (Stearns 1989). Is the optimum clutch size the one which produces the most viable offspring (Lack 1954)? Is there a trade-off between viability of offspring and clutch size, or between survival of the reproducing adult and clutch size? Whichever of these applies, and there is evidence for both kinds of trade-off in birds (Nur 1984; Gustaffson 1988), ultimately the

female will have to make a decision based on the resources available to her and any help she can expect from her partner. It might be predicted that clutch size, and hence reproductive output of a monogamous pair of birds, although set by the female, will be partly dependent on the perceived quality of the male.

If the female gains any direct benefits from a male with a large badge then these benefits should reveal themselves through the superior production of offspring, either numerically or qualitatively. However, a thorough exploration of annual reproduction revealed that females paired with large badged males produced lower numbers of eggs, chicks, fledglings, and recruiting offspring into the subsequent breeding production. Every measure of annual reproductive success was lower in those females mated to larger badged males. If females do prefer large badged males then presumably they must gain something from them. This benefit would have to exceed the disadvantages of a low reproductive output and reduced help with chick rearing.

An alternative, direct benefit a female might gain is a fecundity benefit for her offspring. The "sexy son hypothesis", first proposed by Weatherhead & Robertson (1979), suggests that females may choose to mate with the most attractive males even if they provide less parental care because their reduced fecundity will be compensated for by the higher than average mating success of their sons. The theory relies on two main assumptions: firstly that there is a significant skew in male mating success (through either EPP or polygyny) and secondly that the sexy character has a high heritability. In view of this last assumption, this direct benefit is better dealt with along with the indirect benefits of female trait preference. The two most widely posited indirect benefits a female can gain are, good viability genes, and/or sexiness genes for her offspring. Of these, it is easier to demonstrate genes for sexiness.

Several studies have shown evidence for genetic inheritance of a male sexual trait. If such a trait is indeed sexually selected and thus preferred by female choice then it would pay for females to gain these genes for their offspring. Such a process underlies Fisher's process of sexual selection (1930), with preference and trait genes becoming linked and running away in unidirectional selection. More stable models of sexual selection can also account for trait expression and preferences such as the indicator model of Hamilton & Zuk (1982). In a cross-fostering study of the great tit, Norris (1993) found that sons appeared to inherit breast stripe size from their father and

additionally there did appear to be some inheritance of general viability. In the house finch another sexually selected plumage trait was found to be highly correlated between fathers and their offspring, colour, although in this study there was no cross-fostering and the results could be due to a phenotypic correlation (Hill 1991).

In the house sparrow, we would predict that if female preference was based on the seeking of genes for large badge size, then badge size should have a degree of heritability. This hypothesis was thoroughly tested following the approach of Norris (1993) see above. In 1995 nearly all offspring were cross-fostered, which enabled us to separate environmental and genetic components of heritability. Against expectation, in our population it was discovered that badge size has no genetic heritability. Furthermore, it appears that this trait is environmentally determined, with a highly significant correlation between the badge size of a son and his foster father. This is the first example of non-genetic inheritance of a sexual trait. The mechanism behind this non-genetic inheritance is currently obscure but could, for example, be mediated through some form of social nepotism within the autumnal flock. Regardless of the underlying mechanism, the demonstration that a female could exhibit some control over the size of her sons' badges through her mate choice will have important implications for sexual selection in the house sparrow.

8.2.4 The search for good genes

The idea that female preferences exist for males with the most showy sexual ornaments and the viability genes they are predicted to reveal, is arguably one of the most challenging topics amongst evolutionary biologists. In the absence of known quantitative trait loci, the only way to 'see' viability genes is to attempt to study natural selection taking place. In the laboratory, by definition, many of the external factors which drive natural selection will be removed and hence weaken any selection that may be taking place. In the wild it is difficult to remove enough confounding factors, such as maternal effects and time, to get a clear picture.

To date the only study which has successfully demonstrated unequivocal viability effects of mate choice has been carried out on a lekking species - perhaps the most famous example of sexual selection - the peacock. Petrie (1994) found that the offspring of males with the longest trains do indeed grow significantly faster and survive significantly longer than average (earlier work had already established a female preference for the size of male trains and the

number of eyespots on them (Petrie & Williams 1993)). Perhaps it is no coincidence that in this species there is no male input into reproduction after fertilisation.

In monogamous species it is quite probable that genetic benefits will be limited, or at least obscured, by parenting effects. To date, using the same approach that we used, only a group working on the collared flycatcher in Gotland, a large island in the Baltic Sea, has come close to providing unequivocal evidence for viability benefits of female preferences for specific male traits. Sheldon et al. (1997) demonstrated that the difference in the forehead patch of the two sires, within-pair and extra-pair, of multiply sired broods is positively correlated to fledging condition, i.e. the condition of offspring is predicted by the size of a male sexual trait. Although far from conclusive (due to small sample sizes), the collared flycatcher study is the best evidence for female choice based on viability benefits in a species with biparental care.

Unfortunately, the absence of EPP in the Lundy population prevented the investigation of viability genes and fitness using this approach. Extra-pair offspring provide a natural experiment, with broods consisting of half-siblings therefore removing maternal effects from the comparison and will also mean that the phenotype of the two fathers (genetic and foster) is likely to be different . The more crude approach of simply comparing the fitness of cross-fostered offspring with their genetic and foster parents calls for a much bigger sample to remove maternal effects and ensure that there is a large sample in which the phenotype of genetic and foster fathers is significantly different. Given the time scale of this research, it was not surprising that no clear results on the viability of offspring and the phenotype of their father, either positive or negative, were forthcoming.

8.2.5 The male perspective

We have seen that from the female viewpoint, there appear to be no direct benefits from pairing with a large badged male. The only potential indirect benefit is apparently that, through some unknown mechanism, their sons will have a badge of a similar size to their mate. The question that remains is what does badge size mean to a male?

The 'status-signalling' model was first proposed by Rohwer (1975), to explain plumage variation in the Harris sparrow (*Zonotrichia querula*), which is very

similar to that in the house sparrow, in both the form of the plumage trait and the variation observed within the male population. The model was further elaborated by Maynard Smith & Harper (1988) and evidence was found by Møller (1987a,b) that the badge of the male house sparrow is used in male-male interactions. Males with large badges are more dominant than those with small badges. According to Møller, and the 'Trojan sparrow' model of Owens & Hartley (1991), the honesty of the signal is maintained socially by frequent challenges of those sparrows with the larger badges. A male can only afford to have a large badge if he can withstand these constant threats. Møller carried out his work on social signalling during the winter and this is the time of year during which many (all on Lundy), birds live together in a close flock. If there is a relationship between badge size and dominance on Lundy then we would predict that males with large badges will have higher overwinter survival, as they will have greater access to resources such as food and roosting sites. When we tested this hypothesis it was found that males with large badges do indeed have a greater chance of surviving overwinter (the period of highest natural mortality pers obs.).

The higher social dominance of large badged males and their higher overwinter survival suggest that having a large badge is socially advantageous to males. In contrast, we have already shown that annual reproductive success is lowest in these large badged males. Higher annual survival of large badged males, however, may lead to greater lifetime recruitment of offspring into the breeding population. The implications of this possibility for sexual selection in the house sparrow can be examined through a model which predicts lifetime reproductive success.

8.2.6 Model of male lifetime reproductive success

To fully understand the significance of the house sparrow's badge to sexual selection it is important to measure lifetime reproductive success. This can be achieved by constructing a model which accounts for annual reproductive success and the survival of males with particular phenotypes. The main assumptions made by the model are that badge size is consistent between years and that fecundity and survival are independent of age.

8.2.7 The model

Definition of terms:

LRS	Lifetime reproductive success
S	Probability of annual survival
R	Predicted number of recruits per year

Example of the model assuming a maximum life span of n years for male house sparrows:

$$LRS = R \ (S^1+S^2+S^3......S^n)$$

Either linear or logistic regression can be used to analyse the relationships between badge size and overwinter survival, and badge size and recruitment rates (see Figures 8.1 and 8.2). Linear regression is perhaps the more conservative method but unrealistically the line of regression passes through the zero axis and produces negative values for the number of recruits of very large-badged males. Negative values are not produced if logistic regression is used, although this method is slightly more prone to error with small sample sizes. Both methods are presented. (The analyses from which the components of these models come are presented in full in Sections 4.4.3 and 6.4). The actual regressions presented here vary slightly from those reported earlier due to different datasets however this will have no effect on the construction and outcome of the model.

Figure 8.1 Linear and logistic regression illustrating the relationship between the probability of overwinter survival and male badge size.
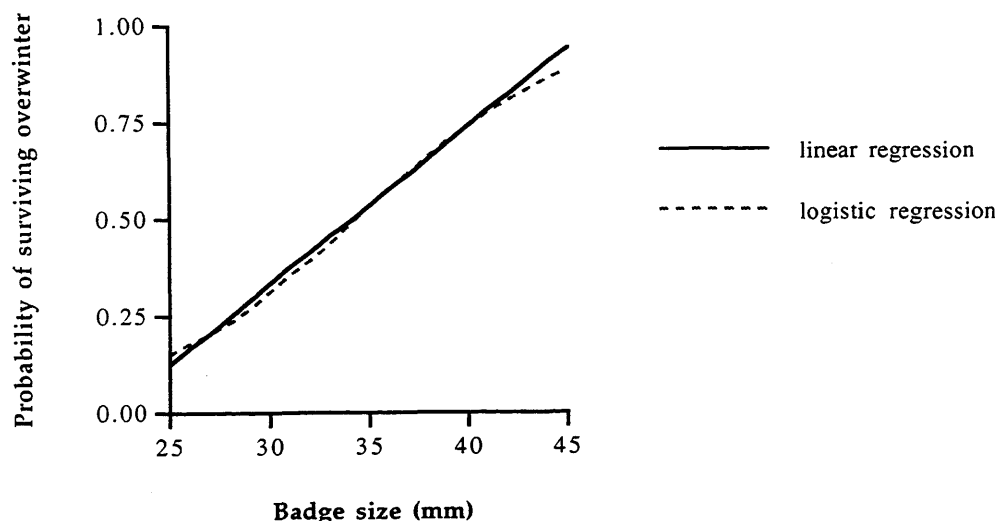
Linear regression: y = -0.901+0.041*badge size
Logistic regression: y = exp(-6.455+0.187*badge size)/(1+exp(-6.455+0.187*badge size))

Figure 8.2 Linear and logistic regression illustrating the relationship between the predicted annual production of offspring recruiting into the breeding population and male badge size.
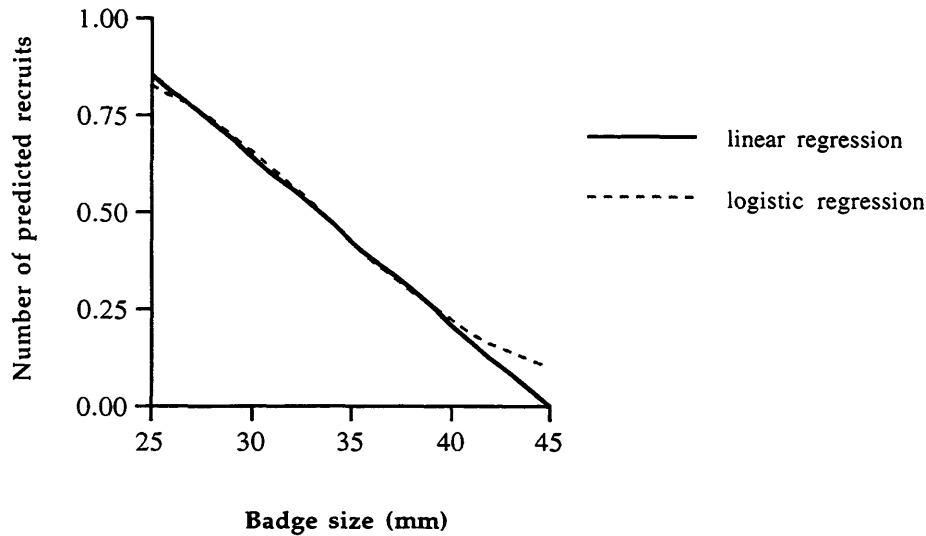
Linear regression: y = 1.935-0.043 * badge size
Logistic regression: y = exp(6.322-0.189*badge size)/(1+exp(6.322-0.189*badge size))

The model for male lifetime reproductive success can be constructed using either the linear or logistic components for S and R (Figures 8.3 and 8.4).

The model yields different results dependent upon the number of years that is permitted for total lifetime expectancy. The model has been calculated with maximum lifetime expectancy for each of one to nine years to illustrate this point. In the Lundy population there are some individuals of at least six years of age, and therefore all models under this value are clearly inapplicable. Nine was used as a maximum age and although it is possible that some individuals could potentially reach a greater age, the effects accounting for greater ages are negligible.

Figure 8.3 Model of total lifetime reproductive success based on linear regression analyses and illustrating maximum life expectancies from one year to nine years.
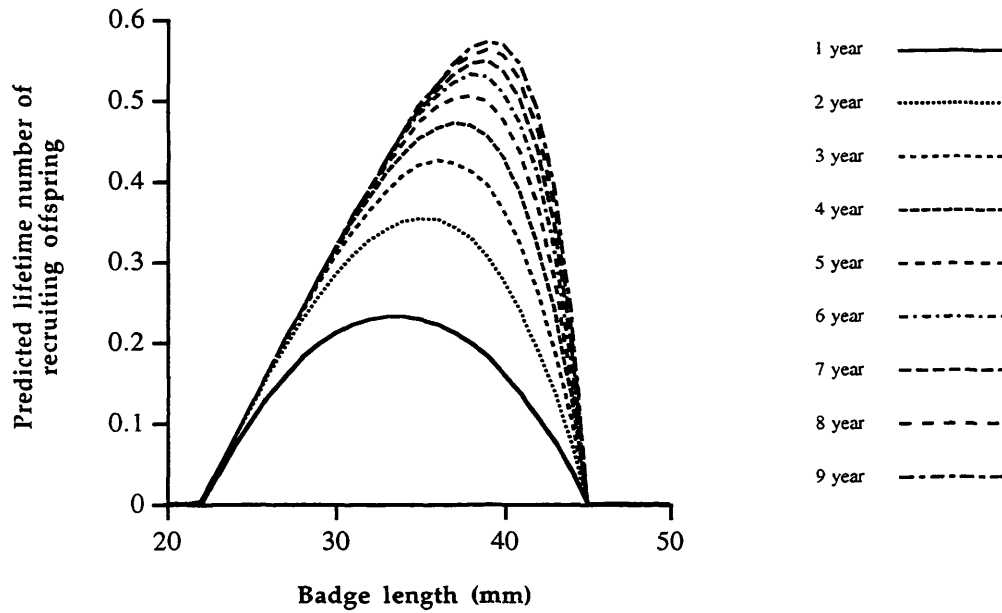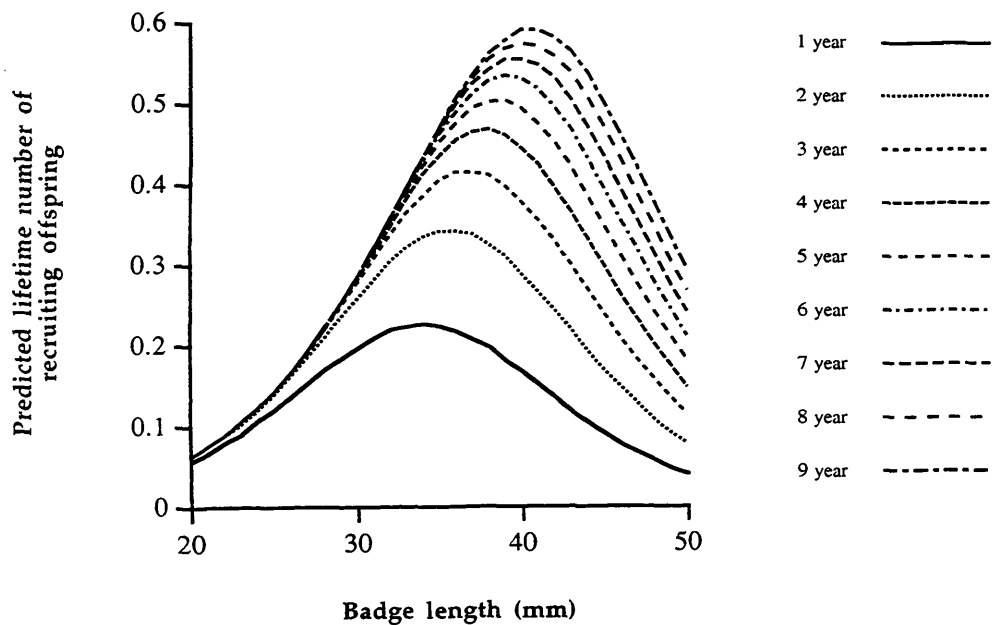

Figure 8.4 Model of total lifetime reproductive success based on logistic regression analyses and illustrating maximum life expectancies from one year to nine years.

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The two models are both highly dependent upon the maximum number of years allowed for males in the population. If no male lives for more than one year (clearly not the case) then maximum production of recruits is approximately 0.2, if nine years is taken to be the maximum life span then the maximum lifetime reproduction will be almost 0.6 recruits.

Figure 8.5 Model of total lifetime reproductive success based on linear and logistic regression analyses and a maximum life expectancy in this population of six years
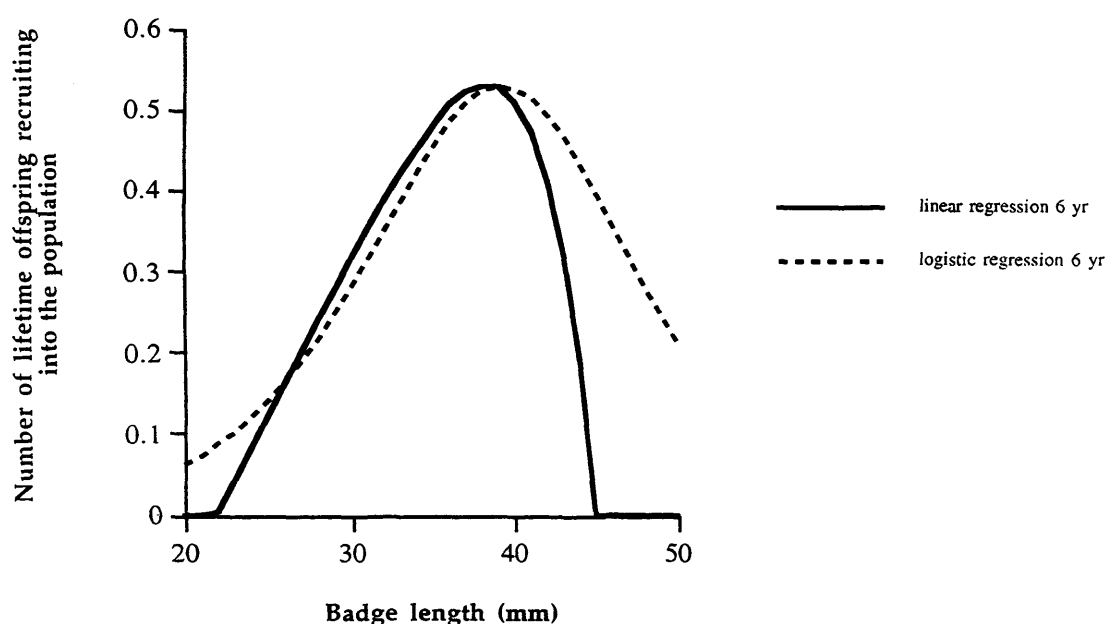
The slope of the regressions for both annual reproductive success and annual survival will have profound implications for the final model. The exact nature of these implications, whilst interesting is outside the scope of this thesis. The construction of this model was purely to determine whether there was, as might be expected, an optimal male badge size. Likewise, whether the model is constructed using linear, or logistic regression analysis is not that crucial. In either case what we are particularly interested in is not the actual empirical predictions that can be made but the overall picture which is revealed. In this respect both models are similar; crucially, both models give an optimum badge size for maximal reproductive output (Figure 8.5). The finding of such an optimal size is crucial to most theories of sexual selection as it will explain the maintenance of the trait. Males with a badge larger than the optimum size will gain no reproductive advantage through their lifetime, as will males with a badge size smaller than the optimum. The exception to this is where conditions change locally to increase or decrease the power of social signalling.

The model and the data on which it has been based suggest that there is some form of trade-off between annual reproductive success and annual survival. Such a trade-off could exist through several mechanisms. Firstly males may operate a strategy in which they trade-off annual versus lifetime survival (the lazy male strategy), assuming that there is a cost to providing parental care (a reasonable assumption (Daan et al. 1996)). Secondly, the relationship between badge size and parental care may be due to condition dependence or else be a signal to females so that they can anticipate the amount of help they will receive (Wolf et al. 1997). Either way, the process could be maintained through genetic polymorphism in the population, or through an evolutionarily stable strategy with males capable of choosing one strategy or the other dependent on circumstances.

The badge and reproductive behaviour may be more implicitly linked. Recent work on the dark-eyed junco (*Junco hyemalis*) has demonstrated that there is a strong link between the expression of a sexual trait and levels of testosterone. Furthermore, testosterone levels have been shown to have a negative effect on many aspects of parental behaviour, including feeding of chicks (Enstrom et al. 1997; Raouf et al. 1997) and the seeking of extra-pair copulations. It has been demonstrated through an experimental manipulation that in the house sparrow that there is a negative relationship between chick feeding behaviour and the level of circulating testosterone (Hegner & Wingfield 1987). In their study, Hegner & Wingfield also demonstrated a significant decrease in the reproductive success of males with an increased level of testosterone, due to starvation of their chicks. Most importantly they also found an increased level of aggression between testosterone high males. Together with the growing evidence of a link between testosterone levels and badge size in the house sparrow (S. Norris & A. Goldsmith, pers comm.) it would appear that the trade-off in males between male-male competition success and reproductive success is hormonally mediated through testosterone.

8.2.8 The final story

From the work conducted for this thesis it is possible to draw several conclusions about sexual selection in the house sparrow:

In this population, at the time of study:

- Alternative mating strategies are uncommon and the effects of EPP on sexual selection will therefore be negligible.

- There appear to be no direct benefits to females of pairing with large-badged males; direct benefits would actually be realised by females pairing with small-badged males.

- Variation in the expression of the badge of the house sparrow has no additive genetic variation and is largely determined by unknown environmental components.

- The only apparent indirect benefit to a female house sparrow from mate choice is that the badge of her sons is similar to that of her male partner (though the mechanism is unknown).

- Male badge size does appear to play a role in social signalling, with large-badged males having greater overwinter survival than their small-badged counterparts.

- Overall lifetime reproductive success, as predicted by a model, will favour neither small-badged or large-badged males but an optimal size between the two.

In summary, adaptive female choice will favour either those males with small badges due to the direct benefits that they provide, or those with optimally sized badges due to the indirect benefits that will be achieved (their sons will have optimally sized badges). Female choice will only be predicted to favour large-badged males under certain circumstances such as in a situation where dominance is currently very important, for example, perhaps where there is restriction of nest sites or food. The possibility remains that female choice for badge size in males does not occur and is not adaptive. This study has failed to produce any clear evidence of a female preference. Ideally, as was initially intended, female choice could be examined through the choice of males as

extra-pair partners (this could be examined through the artificially stimulation of extra-pair paternity by male removals during the fertile period of the female). The choice of males as monogamous partners could be examined through the removal of all males on the island and the late introduction of an experimental set. The time to pairing and nesting would be an accurate reflection of mate choice, this experiment could only be achieved in an ecologically isolated population such as that on Lundy.

Similarly, there is little direct evidence from this study for the occurence of sexual selection through male-male competition although there is some indirect evidence that it may occur. This is another area which would benefit from further experimental study. Dominance hierachies amongst males throughout the year will obviously play a major role in sexual selection and affect within-season reproductive success and survival across years. Badge size manipulations and examination of male-male interactions over resources would greatly increase our understanding of male-male competition in this population.

Finally if we assume that the badge of the house sparrow is a sexually selected trait, through the use of modelling it is suggested that two forms of sexual selection, female choice of a male trait, and male-male competition mediated through the same trait can work antagonistically and concurrently. If this is the case then it will be one of first cases in which one form of sexual selection is working antagonistically with another. This should serve as a cautionary note to others that it is unwise to assume that a trait favoured by one form of sexual selection will automatically by favoured by another.

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