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SEXUAL SELECTION IN THE HOUSE SPARROWS OF LUNDY

By

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Since 1990 the house sparrows (*Passer domesticus*) on Lundy have been the focus of research into sexual selection. Between January 1995 and December 1997 this work has been particularly intensive, being the focus of my doctorate thesis. This article is a brief summary of the work that has been completed to date. The majority of the work will be published in greater detail elsewhere.

INTRODUCTION

When Darwin first published his theory of evolution by natural selection (Darwin 1859) certain traits, such as the tail of the peacock (*Pavo cristatus*), were highlighted by critics. The peacock's long tail is unlikely to increase the chances of survival; in fact, it is more likely to be disadvantageous, with those individuals with the longest tails more likely to be caught by predators. The theory of natural selection was seemingly at odds with the existence of such outrageous, ornamental traits, and in answer to this paradox Darwin proposed the theory of sexual selection which is defined as "the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction" (Darwin 1871).

In the context of this study sexual selection is defined as the difference in the number of progeny that individual male sparrows within the population contribute to the next generation. Theory predicts that some sparrows will be successful and leave many offspring while others will leave very few or none at all. For comparison, in the peacock sexual selection operates through the choice by females of those males with the longest and most 'showy' tails. In addition to mating with these showy males more often, female peahens also lay more eggs after they have mated with a showy male. The result of these two effects is that the showiest males will probably father the majority of the offspring in a given population (Petrie & Williams 1993).

Although obviously not as showy as the peacock, the male house sparrow has a secondary sexual signal that is apparently as appealing or 'sexy' to a female sparrow as the peacock's tail is to the peahen (Møller 1987). This signal, found only in the male, is the black throat patch (referred to as the badge). Within any population of house sparrows there is great variation in the size of this badge between different males. Theories predict that if females find large badges 'sexy', then those males with the largest badges must be better than other males and will therefore produce more offspring. This leads to a skew in the reproductive success of different males. In the house sparrow this skew will operate through a different mechanism than that in the peacock. The peacock has a mating system in which the offspring are reared only by the female. Once a male has copulated with a peahen he will play no further part in the production of offspring; the female nests alone, incubates the eggs and looks after the chicks. In the peacock a female only needs sperm from a male and is therefore free to mate with several

males and is said to breed polygynously. By contrast, the house sparrow mates monogamously. A male and female will generally remain together for a whole summer and often longer. The male participates in nest building, defence of the nest, and contributes just under half of the feeds delivered to the chicks in the nest.

For many years it has been thought that this mating system was a 'perfect marriage' between the two birds. In recent years however it has transpired that all is not quite as it seemed. DNA fingerprinting has revealed that some of the offspring in a male's nest are not actually fathered by him but by another male. Such young are termed 'extra-pair' offspring and have been shown to result from the female actively seeking out males other than their partner to copulate with. Studies in a wide variety of species have shown much variation in the levels of extra-pair paternity. The reed bunting *Emberiza schoeniclus* was found to have an overall level of 55% extra-pair offspring in one study (Dixon *et al.* 1994). This means that on average just over half of the chicks in a nest were not fathered by the male who reared them. The males that father these extra-pair chicks will obviously benefit by siring additional young that will be looked after by another unsuspecting male. The benefits to females of seeking these extra-pair copulations have never been quite so clear, particularly as they risk losing their own partner if he should discover their infidelity.

The aim of this study was to use the house sparrow as a model species to investigate extra-pair paternity, addressing the following questions: Which females indulge in extra-pair copulations? What are the likely benefits to females of participating in extra-pair copulations? Which males lose some of the paternity in their nests? What are the consequences of being an extra-pair offspring? What do female house sparrows see as a 'sexy' male sparrow?

METHODS

During the course of this study all of the individual sparrows on Lundy were caught in mist nets, walk-in traps or nest box traps. They were all ringed with a metal ring supplied by the British Trust for Ornithology (BTO) and a unique combination of three plastic colour rings. The colour ring combinations enabled the author to identify all individuals by sight. When birds were caught several morphological characteristics were measured including: wing length, tarsus length, weight, and the badge size of males. Nest boxes were erected in Millcombe valley woods and the lambing shed and by 1996 over 95% of breeding attempts took place in them. Nest boxes permitted easy access to the nests thus allowing the author to record the success of breeding attempts and also to measure and ring all chicks. In the three years of study over 500 adult and juvenile sparrows were rung. The size of the adult breeding population averaged approximately 40 pairs.

To detect any extra-pair paternity, DNA fingerprinting was carried out at Leicester University using a small blood sample that had been taken from all the studied individuals. The process used was identical to that currently used by forensic scientists to conduct paternity testing in humans and analyse samples from crime scenes. It enabled the author to check, for each offspring, that the male and female feeding the chicks were in fact the real genetic parents and hence whether or not offspring were the product of an extra-pair mating.

One of the main benefits of working on Lundy was that this population was effectively isolated from other populations on the mainland. It is very rare for house sparrows to make the flight across to the mainland and vice-versa. Records from the 1950s and 1960s, when sparrows were absent as a breeding bird from the island, indicate that immigration took place at a

low rate of approximately two birds every three to four years (from Lundy Field Society Annual Reports). It follows therefore, that the sparrows on Lundy will spend their whole lives there. There are very few studies anywhere that rival this in the ability it has to monitor birds' individual life histories to this detailed level. Because all pairs bred in nest boxes the production of eggs and fledglings could be monitored, and all visits to the nest by the male and female were recorded. It was possible to monitor the survival of individual birds. For example, at some point during the day all of the sparrows on Lundy visited the chicken run to feed off scraps left by the chickens. By monitoring this area and a couple of similar areas for a week and recording the identities of all visiting birds, it was possible to determine whether individual birds were alive, or by their absence, dead. By conducting surveys throughout the year it was possible to record the life-histories of all birds. Measuring the life span of individual males and females and all their offspring gave an insight into the reproductive success of adults (there is little point in producing lots of offspring if none of them survive), and also allowed an examination of the relative quality of adults. Were some types of adult better equipped to survive than others? Were some males better parents than others?

RESULTS AND DISCUSSION

The main result of this study was finding that the house sparrows of Lundy have an extraordinarily high level of mate fidelity. Only three of over 300 offspring were not fathered by the male who reared them. This gives a level of extra-pair paternity of less than 1% on Lundy in comparison to 14% for a population of house sparrows in Nottingham and 11% for a population in Kentucky, USA (Wetton & Parkin 1991; I. Stewart pers. comm.). The reason for this low level of infidelity is unclear, but it may be due to the isolated nature of the population. If the population is inbred to any degree then it is possible that all the males will be much the same. A female paired to one male will have little to gain by seeking a sly copulation with another, and therefore the potential costs of seeking an extra-pair copulation will outweigh the benefits. The costs of extra-pair copulations to a female will include the risk of catching a sexually transmitted disease and the loss of her mate should he discover the infidelity. The finding of this low level of extra-pair paternity in the Lundy population is significant, being one of very few examples where extra-pair paternity is such an exceptional occurrence in a monogamous passerine. It is hoped that further examination of this discovery will help to reveal the mechanisms underlying extra-pair paternity.

The rest of this study focused on the badge size of male sparrows and how this relates to the reproductive potential of the male. The reproductive potential of any individual will depend on how successful they are as a parent in any one year and also in how many years they are likely to breed (ie. how long they will live). Many of the theories of sexual selection predict that male sparrows with large badges would have higher annual reproductive success but will suffer higher annual mortality: sexual selection balanced with natural selection. The balance of sexual against natural selection is important because it is one explanation for the current stability of badge size. If males with large badges were favoured by both sexual and natural selection then badge size would surely get progressively larger in each subsequent generation.

As before it was discovered that males with large badges produce less young than those with smaller badges; their female partners lay fewer eggs and consequently they do not produce as many fledged offspring. In addition, it was demonstrated that the young from these males were not as viable and were more likely to die before they are old enough to breed

themselves. This may be partly explained by the fact that large-badged male sparrows were not such good parents and feed their offspring at a significantly lower level than males with smaller badges. Why large-badged males feed their chicks at a lower rate is currently unknown.

Despite being such poor fathers it was discovered that males with large badges had a significantly higher chance of over-winter survival than other males. Therefore it is possible that by being 'lazy' during the summer they directly increase their ability to survive over the winter. Alternatively, there could be something intrinsic about a male with a large badge that makes him better at surviving but worse at parenting.

The conclusion of this study is that males with large badges, conventionally predicted to be 'sexy' and hence more productive, in fact produce fewer offspring on an annual basis but have an apparent advantage over other males in terms of survival. As well as providing empirical support for theoretical models of sexual selection this study provides a good contrast with other studies of sexual selection in birds. The overall theory of sexual selection is supported and interestingly the mechanism is opposite to that which has been revealed in other species i.e. sexy males do not have high fecundity and low survival but instead quite the opposite, low fecundity and higher survival.

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