THE SECRET LIFE OF THE LUNDY HOUSE SPARROWS

by
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ABSTRACT

The House sparrows (*Passer domesticus)* on Lundy have been the subject of continuous study for 26 years. As an effectively closed population, they permit the testing of hypotheses concerning the evolutionary advantages and disadvantages of extra-pair copulation ('infidelity'). This paper summarises the research of recent years which shows that some hypotheses which seek to account for infidelity in House sparrows are not supported by the Lundy data and that other, novel, hypotheses will need to be tested in the future.

Keywords: *House sparrows, Lundy, extra-pair, infidelity*

INTRODUCTION

The Lundy sparrows have been under scientific scrutiny since 1991, when the first nest boxes were erected on the island. Since then, researchers from UK, German and Australian universities have returned every year to closely monitor the Lundy sparrows' breeding success by counting their eggs and chicks, ringing the chicks, and following their fate through their whole life. House sparrows are ubiquitous across the UK (Summers-Smith, 1963) meaning we could catch them in any farm or city. So why specifically study the sparrows on Lundy? Primarily, the geographic isolation of Lundy, combined with its modest sparrow population size mean that we can capture and sample every sparrow that is born on Lundy, and track these individuals throughout their lives. The lack of dispersal in conjunction with the comprehensive monitoring allow us to learn about a rather secretive, yet common behaviour of passerines: infidelity.

Theoretical background

Social monogamy – where a single female and male pair up together to care for one or more broods – is widespread among birds. Yet, the advent of paternity tests using molecular genetics to find out for sure who are the parents of an individual has shown that many male passerines care for someone else's young in their nests, so called 'extra-pair' offspring (Burke & Bruford, 1987). Many socially monogamous passerines display extra-pair behaviour, meaning they mate with birds other than their social partner (Griffith, Owens & Thuman, 2002). Males that sire extra-pair offspring are thought to increase their breeding success at little or no cost, because they do not provide parental care, incubate the eggs, and bring food to these extra-pair offspring (Schroeder *et al.*,

2016). In addition, males can increase their reproductive output by fertilising more females, because sperm are far less costly to produce than eggs (Birkhead, 2000). So males can fertilise, or attempt to fertilise, a large number of females. Females, however, are limited in the number of eggs they can produce and the number of offspring they can care for. In sparrows, a brood usually has no more than four to a maximum of six eggs. Thus, if females cheat on their social mate, their reproductive output is the same; they produce an offspring sired by their extra-pair partner (an extra-pair offspring) instead of one sired by their social partner (a within-pair offspring). Therefore, female reproduction is inherently limited, but male reproduction is much less constrained.

Even if females were to dump their eggs into a strangers' nest (something we have never observed in Lundy sparrows), the energetic investment that a female puts into the production of an egg by far outnumbers what a male invests into a sperm. Therefore, a basic assumption in evolutionary biology is that males invest in quantity of offspring, while females invest in quality (Kempenaers & Schlicht, 2010).

Hypotheses

The dichotomy in how much each sex can increase their breeding success has inspired more than two decades of research. It seems obvious why males would cheat (to have more offspring at little cost), yet it remains unclear why females cheat. One hypothesis (see Forstmeier, Nakagawa, Griffith & Kempenaers, 2014, for a review and summary of all stated hypotheses), called the 'good genes' hypothesis, states that females who produce extra-pair offspring gain indirect genetic benefits because they choose extra-pair males of higher quality than their social partner. Thus the offspring sired by an extra-pair male with 'good genes' are expected to inherit his higher genetic quality. A second hypothesis – the genetic compatibility hypothesis – states that extra-pair males are not genetically superior to the social partner, but are instead more compatible with the female's own genome. For example, if a female socially mated with a close cousin as a social partner, she could have poor quality offspring, and she might therefore choose an unrelated extra-pair partner to have higher quality extra-pair offspring.

Predictions

The above described two hypotheses clearly predict that within-pair offspring should be of lower quality than extra-pair offspring, and thus we expect within-pair offspring to have lower fitness (e.g. lower survival and reproduction rates) than extra-pair offspring. In addition, the good genes hypothesis predicts that extra-pair males are better than within-pair males. The genetic compatibility hypothesis predicts that extra-pair males are more genetically dissimilar from the female than the within-pair male. To test these predictions, we first need to know which offspring are extra-pair and who the extra-pair father is, which can be determined with a genetic paternity test (Dawson *et al.*, 2012).

The cheating Lundy sparrows

It is relatively easy to show that a social father is not the genetic father of an offspring. If, after accounting for the maternal genotype, the alleles do not fit with the genetic make-up of the social father's genotype, it is clear that the female must have cheated. However, identifying the actual genetic father can only be achieved if the extra-pair father is also DNA-sampled. Herein lies the crux of why we study sparrows on Lundy

island. In an open population, birds can fly freely to and from the study area, hence many extra-pair fathers are simply not caught and genotyped by chance. The vast majority of Lundy sparrows stay on the island, and we can capture and sample every bird. Thus, it is unlikely that resident sparrows leave the island, or mainland sparrows immigrate to Lundy regularly (Schroeder, Burke, Mannarelli, Dawson & Nakagawa, 2012). Therefore, in the Lundy sparrows, it is possible to genetically identify each and every extra-pair father. Prof. Terry Burke from the University of Sheffield has, as early as the 1990s, recognized that Lundy is an ideal and unique natural laboratory to test the above-mentioned hypotheses for why females cheat.

RESULTS OF LONG-TERM LUNDY SPARROW RESEARCH

After two decades of research on Lundy, we can rule out some of these hypotheses. The indirect fitness benefits hypothesis predicts that extra-pair males should be of higher quality than within-pair males. Furthermore, it also predicts that extra-pair offspring will do better in life than within-pair offspring, because they received the good genes from the extra-pair fathers. Of the three studies that used lifetime reproductive success to study this question, one supported the indirect fitness benefits hypothesis (Gerlach, McGlothlin, Parker & Ketterson, 2012) while two opposed it (Hsu, Schroeder, Winney, Burke & Nakagawa, 2014, and Reid & Sardell, 2011). Our own long-term data from the Lundy sparrows goes against the indirect fitness hypothesis entirely; our work shows that extra-pair offspring have a lower survival than within-pair offspring (Hsu, Schroeder, Winney, Burke & Nakagawa, 2014), and so are clearly not of higher quality. From the genetic compatibility hypothesis, we can predict that that within-pair males should be more closely related to the female than the extra-pair males. The evidence from other passerine populations is inconclusive (Hsu, Schroeder, Winney, Burke & Nakagawa, 2015, and Arct, Drobniak & Cichon, 2015). On Lundy, extra-pair males and within-pair males do not differ in how related they are to the female (Hsu, Schroeder, Winney, Burke & Nakagawa, 2015). In fact, the only difference is that extra-pair males are older than within-pair males (Hsu *et al.*, 2017). Therefore, Lundy data also does not support the hypothesis that females engage in extra-pair copulation to reduce inbreeding in their offspring (Hsu, Schroeder, Winney, Burke & Nakagawa, 2015). Thus, our data suggests that engaging in extra-pair behaviours is not adaptive for females. Clearly, we need new hypotheses.

A fresh perspective

Recently, other researchers have put forward a number of novel hypotheses that do not require female extra-pair behaviour to be beneficial (Forstmeier, Nakagawa, Griffith & Kempenaers, 2014). These have been called non-adaptive hypotheses. The sexually antagonistic selection hypothesis suggests that a gene for extra-pair behaviour may be beneficial in males but not in females. If the genes are selected for in males, this may lead to female extra-pair behaviour as a by-product (Forstmeier, Nakagawa, Griffith & Kempenaers, 2014). The spill-over hypothesis suggests that female and male infidelity is a spill-over effect for individuals with high sexual activity levels. Females and males with a high sex drive may engage more in mating and thus may be more likely to engage in extra-pair mating attempts too (Forstmeier, Nakagawa, Griffith & Kempenaers, 2014). A similar hypothesis, the opportunity hypothesis, suggests that female and male

infidelity is a by-product of socialising. Spending time in the close vicinity of others may have benefits such as greater protection from predators, higher chance of finding food sources etc. However, the same behaviour may also bring with it a weaker pair bond and plenty of opportunities for extra-pair copulations. This is particularly interesting in sparrows that form social groups during and outside their breeding season. In the future, we will continue conducting research on the Lundy sparrows, focusing on these novel hypotheses. We are confident of gaining a fresh perspective on infidelity by studying how these charismatic birds spend time with each other.

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