# Sexual selection and reproductive strategies in songbirds

Berg, Mathew Leslie

# Summary

## EVOLUTION AND REPRODUCTIVE BEHAVIOUR

Variation in reproductive strategies is incredibly widespread throughout the animal kingdom. Consequently, the study of how individuals allocate resources such as time and energy to various aspects of reproduction is central to understanding life history strategies and the diversity of life. Since the 1859 publication of Charles Darwin's theory on evolution by natural selection, a basic premise of behavioural biology is that animals will behave in a way that maximises their genetic contribution to future generations. Individuals carrying genes that encode the most successful behaviour will survive longer and/or successfully raise more offspring, which in turn inherit those genes. In such a way, these genes and the behaviour that they generate should proliferate. This means that when individuals are deciding how, when and where to invest in reproduction, they should consider which strategies would give them the greatest evolutionary "return". More specifically, they can accomplish this by adopting strategies that help them to compete with conspecifics for territories and mates, avoid predation and ill-health, and raise successful offspring.

## SEXUAL SELECTION

Sexual selection was first described by Charles Darwin in 1871. It is a form of evolution that deals with the advantage that individuals have over others of the same sex, in exclusive relation to reproduction. Sexual selection is deeply important, because it can cause species to form and diverge, and as discussed in this thesis, can influence individuals at most if not all stages of their life cycle. In birds, this form of evolution generally operates through two main processes. First, strategies will be favoured that make an individual good at competing with other individuals of the same sex (intra-sexual selection). Second, strategies will be favoured that make individuals more attractive to the opposite sex as mates (inter-sexual selection). The competition and conflict that occurs between individuals for such reproductive advantages are at the heart of sexual selection, and the ways in which individuals vary their reproductive strategies in the face of such competition and conflict are major themes in this thesis.

## THE IMPORTANCE OF ENVIRONMENTAL CONDITIONS

In natural systems, variation in the reproductive strategies that individuals adopt at any given time can often be attributed not only to intrinsic traits of the individual (e.g. size, health, condition or energy reserves), but also to variation in their extrinsic environmental circumstances (e.g. food availability, predator abundance, climate, social or mating status). Importantly, different members of a population often experience different environmental conditions, and different individuals may be expected to react differently to different environments. Moreover, many interesting interactions exist between extrinsic and intrinsic factors.

## THE IDEA BEHIND THIS THESIS

Through the studies described in this thesis, we attempted to unravel some of the evolutionary processes behind a range of reproductive strategies of two common species of songbirds. We do this by observing the reproductive behaviour of individuals, using the theoretical basis afforded by sexual selection and with knowledge and manipulations of their environmental conditions (in particular, food availability and social circumstances).

For many research questions about the adaptations of animals in the wild, birds offer an excellent research opportunity. I chose songbirds as the study model, and studied their reproductive behaviour at three key stages of reproduction: defending a territory (Part I), attracting a mate (Part III), and caring for offspring (Part IV). We did this primarily from a male point of view because, in most species, it is the males that compete most intensely and the females that are choosy.

Furthermore, with the advent of DNA fingerprinting techniques, we have learnt that many species of songbirds are genetically promiscuous and commonly produce offspring outside the pair bond (see **Box 1.1**). Therefore, males are expected to implement a range of interesting strategies in order to enhance their certainty of paternity and improve their reproductive success without relying on offspring of uncertain paternity. This can often mean that the variation in reproductive success between individuals within a population is considerably higher for males than for females.

The studies described are based on fieldwork conducted during the breeding seasons from 1999 to 2002 on winter wrens (in The Netherlands) and Australian reed warblers (in Australia). For more information on the study species see **Box 1.2** and for more detailed information on concepts discussed in this summary see **chapters 1** and **10**.

## TERRITORY DEFENCE (Part II)

The first stage in reproduction for most songbirds, as for many other animals, is the establishment of a stable territory or breeding position where reproduction can take place. Territories are a crucial step in reproduction for many species, because they ensure access to resources that are essential for successful reproduction.

Song is widely acknowledged to play a crucial role in territory defence in many birds. In **chapter 3** (with Sanne Boessenkool, Margreet Drijfhout and Jan Komdeur), we found that males wrens could distinguish familiar (neighbouring) and unfamiliar competitors based on their song alone. Further, they responded less aggressively towards songs of their neighbours than to strangers, a phenomenon known as the "dear enemy" effect. Interestingly though, when these males were tested with songs from the same individuals a couple of days later, they responded far less strongly to the songs of the previously unfamiliar males. This shows that male wrens can recognize their competitors from song alone and rapidly adjust how they react to these competitors based on previous meetings. **Chapter 4** (with Jan Komdeur) also deals with the evolution of song as a sexual signal. Given the high incidence of extra-pair paternity in many songbirds, many male strategies

are concerned with maximizing their success at attracting additional mates but minimizing loss of paternity with their existing mates. We found that male wrens engage in counter-singing bouts with intruding males much more vigorously when their mate was fertile, even though they were not generally more defensive of their territory. We think that this may be because females utilize a male's ability to out-sing intruding males to determine the best male with which to mate. Therefore, males should be particularly keen to put in good performances when their mate is fertile and their paternity is therefore at stake.

## MATE ATTRACTION (Part III)

How birds go about attracting a mate has been one of the most intensively studied aspects of sexual selection over the last three decades. When searching for a partner, most females are expected to be concerned with finding the best quality mate possible. The most important features that female birds look for may be things such as health and condition, but these could be difficult for females to assess quickly while choosing a mate. Accordingly, much research focuses on the ways in which males can advertise their qualities to potential mates (both social mates and extra-pair partners). Importantly, if females are to gather reliable information about prospective mates from male advertisements, the signals used for this must be kept honest and difficult to fake.

Aside from territory defence, the other major function of bird song is thought to be mate attraction. **Chapter 5** (with Nienke Beintema, Justin Welbergen and Jan Komdeur) shows how the amount a male is able to sing may work in this vain. By providing supplementary food to a half of reed warbler territories, we show that the amount of food available on the territory has a large effect on the amount that males sing. Moreover, these birds adjusted their singing patterns closely to the amount of food available on a day-to-day basis, showing that male song rate could be a very precise way for females to judge the quality of a male (or his territory) at any given time.

**Chapter 6** (with Nienke Beintema, Justin Welbergen and Jan Komdeur) continues this theme, by describing a novel behaviour in reed warblers that female reed warblers may use to choose their mates. Reed warblers commonly build small nest-like structures on their territories. These structures are only built prior to pairing up, which suggests that they too may be involved in mate attraction. We show that the amount of these structures built increased as more food was available. However, when the pairing success of males was compared to the number of these structures that they had, we found no association. This may be because females use a variety of cues when deciding who to pair with, or because most males are eventually successful in attracting a mate meaning that we were unable to find a difference in overall pairing success.

The benefits to males of mating with multiple females are clear (the chance to sire more offspring), but the benefits to female birds of such promiscuity are less obvious. Because females rarely receive a contribution to the care of the offspring from males outside their pair bond, it is often suggested that they engage in such extra-pair copulations

to secure better genes for their offspring. To investigate this in wrens we developed a microsatellite-based system to genotype (genetically "fingerprint") wrens (**chapter 2**). We implemented this system in **chapter 7**, and found that 19% of wren offspring arose from an extra-pair mating, and that such offspring occurred in 38% of nests. This genotyping system also allowed us to make inferences about the genetic variability and history of family inbreeding of individuals, which we expect to have ramifications for their attractiveness to mates. Indeed, we found some evidence that males with more genetic variability were heavier and in better body condition. Furthermore, we found that less genetically diverse males paired with unfaithful females had a higher proportion of extra-pair young in their nests. Surprisingly, however, less genetically diverse males were less likely to lose paternity to other males in the first place. These intriguing results suggest that the process linking male genetic diversity to mating success are far from simple, and will provide many avenues for future research.

## PARENTAL CARE (Part IV)

If an individual has successfully obtained a breeding territory and acquired a mate, it then has to decide when and how much to care for it's offspring. Parental care is virtually ubiquitous in songbirds, and most species display bi-parental care to some extent (both the mother and the father take part). This care may take several forms, but the most commonly encountered forms in birds are incubating the eggs and providing food to the offspring.

In **chapter 8** (with Jan Komdeur), we examine how males may make use of the possibilities to mate with additional females, even at the expense of caring for their existing offspring. We found that male reed warblers dramatically reduce the level of care they provide to their existing brood when they have more neighbours around them (females did not change their level of care). Experiments showed that probably arises both from the territorial duties that males have, as well as the attention they pay to nearby females (which they probably view as potential additional mates).

In **chapter 9** we examine parental care from a mainly female perspective, in this case incubation of eggs. In Australian reed warblers, only the female incubates the eggs. Using a food supplementation experiment, we showed that the amount of time a female spent incubating the eggs was determined in part by the amount of food that she has available. Interestingly, this also seemed to apply to the period before the clutch was complete, meaning that the first laid eggs tended to hatch earlier than the later eggs. This resulted in a greater size difference between the oldest and youngest chicks in a nest. It's likely that it is easier to both incubate the eggs for more of the time and to raise an asynchronously hatching brood when there is plenty of food available. We think that it might be advantageous for females to adopt this strategy, provided they have enough food available, in order to reduce the period that their offspring spend in the nest where they are more vulnerable to predation by snakes and introduced rats.