Extra-pair paternity in birds

Avian Infidelity

ANNA DUBIEC
Museum and Institute of Zoology, Warsaw
Polish Academy of Sciences
adubiec@miiz.waw.pl

Birds were until recently considered to be very faithful animals, but now we know that "extramarital" affairs are common among most socially monogamous species. What motivates birds to cheat?

The traditional classification of animal mating systems, based on observations of social behaviors, distinguishes betwen several basic systems: monogamy (an exclusive relationship between a single male and a single female), polygyny (one male with two or more females), polyandry (one female with two or more males), and polygynandry (a system in which males and females mate freely but exclusively among the individuals in a group). Bearing only this criterion in mind, it used to be assumed that the male and female forming a socially monogamous pair were the real genetic parents of their offspring. However, in the latter half of the 20th century, once molecular techniques, which enable quick determination of whether a given male is the genetic father of a specific individual, came into widespread use, it became obvious that social monogamy needs to be distinguished from genetic monogamy.

Monika Zielińska

In cooperation with Monika and Piotr Zielinski from the Orinthological Station of the Museum and Institute of Zoology, Polish Academy of Sciences, the author of this article studies extra-pair paternity in house martins

Scandalously unfaithful

The first signals that it might be incorrect to equate social and genetic monogamy came from research carried out in the United States in the 1940s. The study focused on the mechanisms of blood type inheritance in humans and was based on a sample of 1000 infants and their parents. The analyses revealed that in as many as 10% of cases the man tested simply could not be the genetic father of "his" child. However, our understanding of mating systems was truly revolutionized only once molecular techniques became widespread in ornithological studies. In the late 1960s biologists believed that above 90% of over 9,000 bird species were monogamous. Molecular analyses revealed, though, that chicks from sexual encounters between a female and a male who was not her stable social partner occurred in 75% of socially monogamous species. On average, 11% of all chicks are sired by extra-pair males and nearly 19% of broods include at least one chick from an "extramarital" encounter. Among the passerines (the largest group of bird species) in 25% of the socially monogamous species, 25% of all chicks turn out to have been sired by extra-pair males.

Interestingly, sometimes *none* of the chicks reared by the social partner of a female are actually his own offspring, and the brood from a single nest may even include the offspring of a number of males. The most faithful types of birds are owls and sea birds, whereas the most unfaithful are the small passerines: the reed bunting, the red-eyed vireo, and the tree swallow (with even as many as 50% of chicks from extra-pair matings).

Benefits of betrayal

Since its discovery, the phenomenon of extra-pair mating in birds has remained in the focus of biologists' research interests. Since the 1980s, each successive year has brought new information about this and related phenomena in several new species. Scientists are particularly intrigued by the evolution of such mating behavior and its maintenance in nature. From the male perspective, fathering as many extra-pair offspring as

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The starling is among the species that exhibit relatively high levels of extra-pair paternity: 9% of all chicks are of extra-pair origin, whereas as many as 31% of all broods contain at least one such chick

possible is undoubtedly favorable, because he can pass on his genes to the next generation without having to invest in rearing his own young. But the reasons why females engage in extra-pair matings are less clear, especially since females do not produce a large number of reproductive cells like males do. In certain species, such infidelity even entails additional costs, such as reduced feeding rate and nest protection by the social partner, the risk of sexually transmitted infections, and greater susceptibility to predatory attack. On the other hand, unfaithful females may gain the assistance of the extra-pair partner in caring for their chicks and territory defence, as well as insure against the risk of their social partner's infertility. Females may also aim at obtaining "good genes" and maximising genetic compatibility and diveristy of the offspring since they affect the offspring fitness.

Genetic legacy

According to the "good genes" hypothesis, females mate with males that are in better condition and exhibit more favorable secondary sexual traits than their own social partner. Females frequently choose males older than their social partner – longevity may be a sign that a given male is in possession of genes that help to ensure a long lifespan. The genetic compatibility hypothesis states that in the process of mate choice females choose males whose genotypes best complement their own. And maximisation of offspring genetic diversity may be especially important under changing environmental conditions, where various genotypes may be better or worse adapted to a given set of conditions.

One set of genes that is potentially crucial in generating indirect (genetic) benefits from extra-pair matings are genes of the major histocompatibility complex (MHC). These genes code for protein molecules which recognize foreign antigens and present them to T lymphocytes, which in turn triggers the immune response. The more diverse the genes in the complex, the more resistant against the pathogens the offspring will be. The latest research results suggest that mate choice in birds, like in certain mammals and fish, may be linked to olfactory stimuli that depend on the set of the MHC genes a given individual possesses.

Hasty choices

The existence of traits involved in the process of mate selection raises the question of why extra-pair paternity should be so widespread. It may be attributable to limitations and costs associated with finding and assessing the male as a potential partner. Birds, which mate seasonally, are under pressure to proceed with mating as quickly as possible once the season starts; such haste means that pairs are frequently not ideally matched in genetic terms. If a female subsequently encounters a male whose genetic material promises to boost the adaptive potential of at least some of her offspring, she copulates with him. In many species, a female's social partner strives to prevent such extra-pair encounters by copulating with her frequently and guarding her during her fertile period. Even if she does copulate with another male, her social partner still stands a chance of winning the paternity battle as long as he is the last male who deposits sperm into her re-

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The blue tit is an example of the species whose females actively seek out males for extra-pair copulation. Such matings produce 11% of all blue tit chicks, whereas 40% of all broods contain at least one chick of extra-pair origin

productive system just before the egg cell is fertilized. The constant presence of the social partner may deter the female from actively seeking other males, as well as prevent forced copulation attempts by other males in the population.

Interestingly, the frequency of extra-pair paternity varies greatly not just among species, but also among different populations of the same species, and even among different individuals in the same population. On the population/species level, this can only partially be explained in terms of ecological factors such as breeding synchronization and population density: given high synchronization and density of nesting pairs, the costs incurred by a female in seeking out a partner are relatively small, which in turn should promote extra-pair paternity.

Under pressure

Recently there has been an intense debate in the scientific literature about the adaptive value of extra-pair paternity and its maintenance in nature. According to one view, the phenomenon is maintained mainly due to selective pressure on the females, who seek extra-pair matings in order to gain genetic benefits for their offspring. In certain species, females indeed actively seek extra-pair partners - one example being the blue tit, whose females fly over to the territory of neighbors they may mate with. Opponents of this view argue that the direct selective pressure against the active pursuit of extra-pair matings by females is stronger than the indirect pressure on such behaviour. They suggest that the phenomenon instead results from strong selective pressure on the males, who strive to fertilize as many females as possible outside their own pair. And so although it is not fully clear what factors underlie the phenomenon of extra-pair paternity, it has definitely played a significant role in the evolution of avian mating behavior. Undoubtedly, the research on mixed mating strategies in birds will still attract a lot of attention in the future. ■

Further reading:

Westneat D.F., Stewart I.R.K. (2003). Extra-pair paternity in birds: causes, correlates, and conflict. *Annu. Rev. Ecol. Evol. Syst., 34*, 365-396.

Griffith S.C., Owens I.P.F., Thuman K.A. (2002). Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol., 11*, 2195-2212.