Sexual Selection: Copycat Mating in Birds

Female zebra finches may be influenced by the choices of other females when selecting mates, challenging the view that mate-choice copying should not occur in species with biparental care.

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Choosing a mate is not a simple business. A female needs a male in order to reproduce, but how does she know which one to pick? How can she find a good mate without wasting too much time and effort? One answer is to watch what other females are doing and choose the same males, or same kind of males, as they do.

For species in which males do not help care for their young, such mate-choice copying might work very well. Females want the healthiest, most attractive males. and the behaviour of other females might guide them to these males. However, if males help to care for their young and females are searching for a good father, the potential benefits of copying are less clear [1]: a female who copies will have to share the male's parenting efforts with another female. In line with this, evidence for matechoice copying has been restricted to polygynous species of fish and birds with little or no male care [2]. But now, work by Swaddle and colleagues [3] suggests that it may occur in a species with male care too.

The most common experimental set-up for investigating mate-choice copying presents a 'focal' female with two males, one of which is housed with a 'model' female and the other of which is housed alone. The focal female is then given the opportunity to choose between these two males after removal of the model female. Copying is inferred if, in the preference test, the focal female spends more time with the male that was apparently 'chosen' by the model female than with the male that was unpaired.

The most convincing evidence for mate-choice copying comes from an elegant series of experiments on polygynous Japanese quail by Galef and White (reviewed in [4]). These researchers found that female quail spent more time with a male after seeing him mate with a model female. Importantly, their experiments ruled out several alternative explanations, notably that the focal female could have been responding to changes in the mated male's behaviour, or simply favouring a location where more conspecifics had been present. Instead, the female quail were apparently copying the mating decisions of other females.

The new study by Swaddle et al. [3] is an intriguing development because their subject animal, the zebra finch (Figure 1), is a monogamous species with biparental care. In their first experiment, female zebra finches saw one male (the 'mixed-sex male') paired with a model female and another male (the 'same-sex male') paired with a model male. This set-up ensured that the intended difference between the males — that only one of them was paired with a female — was not confounded with a difference in the number of individuals present. After two weeks of exposure to these pairs, the focal females were given preference tests, during which they were found to spend significantly more time with the mixed-sex male than the samesex male. This result is consistent with mate-choice copying.

If females favour males that have successfully paired, what possible benefits could this have in a species with biparental care? In zebra finches, which live in semi-arid regions of Australia, breeding is opportunistic and highly dependent on the availability of seeds produced during short rainy periods [5]. Females that copy the choices of others may reduce the time spent searching for and assessing males, particularly if new breeding opportunities become available as other females switch partners or leave the area [1,3,6]. Alternatively, mate-choice copying may be used by unfaithful females in seeking an extra-pair mating [6]. The new data on zebra finches suggest that the potential benefit of mate-choice copying in species with biparental care deserves more serious investigation.

However, although Swaddle et al.'s [3] data were consistent with mate-choice copying, their experimental design did not control for the possibility that females were responding to a change in the males' behaviour. rather than directly copying the decisions of other females. The focal female observed the pairs for a two-week period, during which time the mixed-sex male was presumably courting the model female and copulating with her, while the same-sex male was interacting with another male. Females may simply have been showing a preference for a more actively courting male. Furthermore, the males' different experiences in this two-week period could easily have generated a behavioural difference in the subsequent preference test. Further experiments, along the lines of those used by Galef and White [4] on Japanese quail, are needed to distinguish exactly what cues are important to females in biasing their mating preferences.

Swaddle et al.'s [3] second experiment is perhaps more

relevant for a monogamous species, as it suggests that females might prefer not the 'chosen' male, but other males that look similar to him. Here, the researchers manipulated male appearance using an artificial trait known to influence mate choice: coloured plastic legbands [7]. The stimulus males were in a mixed-sex or same-sex pair as before, but this time one male wore orange leg bands while the other male wore white. After two weeks' exposure, the focal females were given a choice between an orangebanded and a white-banded male, but these males were different to those they had seen previously. Despite having had no initial preference for one band colour over the other, by the end of the two-week period, the focal females spent significantly more time with unfamiliar males wearing the same colour as the original mixed-sex male.

Whether these data represent a true case of mate-choice copying, or some other form of nonindependent mate choice [8], is not clear. The focal female may have associated the mixed-sex band colour with the presence of another female, or she may have associated this band colour with male courtship behaviour, the presence of a nest or some other cue. Whatever the mechanism. Swaddle et al.'s [3] results show that females can develop a generalised preference for males similar in appearance to those chosen by other females.

Only two previous studies, one on Japanese quail [9] and one on guppies [10], have provided similar evidence that females develop a generalised preference for a male trait by observing the social interactions of other females. Together with Swaddle et al.'s [3] findings, these data open up the exciting possibility that mating preferences might spread not only genetically, as assumed in standard models of sexual selection [11], but also non-genetically, through social learning mechanisms. Copying amongst females, and other

forms of non-independent mate choice [8], could make attractive males even more popular, reinforcing sexual selection on male characteristics and driving their further elaboration.

'Cultural inheritance' of mating preferences may be a potent force in the evolution of attractive male traits and, as such, should be incorporated into standard models of sexual selection [12-15]. Swaddle et al.'s [3] results suggest that it may be important even in monogamous species with biparental care. Given the pervasiveness of cultural influences on mate choice in human beings [12], social influences on mate preferences may be particularly important in the evolution of sexually selected traits in our own biparental species.

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Figure 1. A male zebra finch (left) with two females.