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Mate choice copying in monogamous species: should females use public information to choose extrapair mates?

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Empirical evidence that females can copy each other's mating preferences comes predominantly from research on lekking species, but recent laboratory studies revealed that public information can also play a role in the evolution of mate preferences in monogamous species with biparental care. Although the question of why monogamous females copy each other's mating preferences is still debated, it has been suggested that public information could be used by females to assess and choose extrapair mates. Since there is only indirect empirical support for this hypothesis, I developed a game-theoretic model to explore the possible roles that mate choice copying may play in mediating extrapair behaviours in monogamous species. Like previous game-theoretic models on mate choice copying, the model predicts that only females that have a high probability of obtaining a better partner should copy the mating decisions of others. On the other hand, unlike previous games that applied to lekking species, the present model predicts that mate choice copying can be advantageous even when there is no variation among females in their discrimination ability and they all can assess the quality of potential partners without error. Moreover, as mate choice copying essentially benefits high-quality males, males of lower quality would be interested in developing defensive tactics to discourage females from seeking extrapair copulations, thereby contributing to intraspecific and interspecific variations in the rate of extrapair paternity.

Keywords: ESS model; extrapair copulation; mate choice; monogamous species; public information

A growing number of studies have reported that social environment may influence mate preferences (Westneat et al. 2000). One example of a nonindependent choice is mate choice copying, in which mate preference, typically of a female for a male, causes an increased preference for that particular male in another female. Although the costs and benefits of copying are still poorly understood (Dugatkin 1996), the use of public information, that is information derived from others' mating interactions and decisions (Danchin et al. 2004), could provide females with information about a larger number of potential partners or with more reliable information about their relative quality (Nordell & Valone 1998). Thus, mate choice copying might be beneficial when mate assessment is time-consuming or error-prone. Females from the lekking species, for example, may benefit from copying others' choices while incurring little or no cost: males have little to offer to females aside from sperm and sperm can be shared over several females (e.g. White & Galef 2000). This is particularly true if copier females do not reproduce immediately after having observed another female mating with a particular male, as sperm can be stored again during the time interval (Westneat et al. 1998), and copier females may then not face higher risks of sperm depletion than noncopying females.

Although mate choice copying provides the same benefits to females from monogamous species, it also imposes severe costs: the breeding performance of a female then strongly depends on her mate's assistance, through breeding resources and paternal care. Yet recent laboratory studies revealed that public information may also play a role in the evolution of mate preferences in monogamous species with biparental care (Doucet et al. 2004; Swaddle et al. 2005). The most convincing evidence for mate choice copying in monogamous species comes from experiments on zebra finches, *Taeniopygia guttata* (Swaddle et al. 2005). Swaddle et al. clearly indicate that females may acquire preferences for particular males that

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had been observed to be successful mates. The question of why monogamous females copy each other's mating preferences, however, is still debated. A possibility is that females from social monogamous species use public information to accept (or reject) males similar in appearance to those that have been most frequently accepted (or rejected) by other females (Swaddle et al. 2005), a form of copying that may lead to cultural inheritance of mate preferences (Brooks 1998). Another possibility is that monogamous females solicit extrapair copulations (EPCs) with already mated males (Doucet et al. 2004).

Some laboratory experiments provide support for the hypothesis that monogamous females can acquire a preference for generalized traits rather than particular males only. Indeed, Swaddle et al. (2005) found that female zebra finches preferred new males that were wearing the same leg band colour as the apparently chosen males. On the other hand, no theoretical or empirical study has yet directly investigated the possibility that public information could be used by monogamous females seeking extrapair males. Only indirect evidence supports the hypothesis that monogamous females could use mate choice copying in extrapair mating decisions. Indeed, several studies reported that the timing of pair formation may affect both the female's choosiness and the probability that the pair's nest would contain an extrapair young. For instance, Johnson et al. (2002) found that male house wrens, *Troglodytes aedon*, in pairs formed early in the season are of higher quality and are less cuckolded than males in pairs formed later. These results suggest that less selective females form a pair bond with a social partner of low quality but display active choice of the extrapair partners by seeking copulations with already mated males that had been observed to be successful mates. In addition, the results from Slagsvold et al.'s (2001) experiments indicate that female pied flycatchers, *Ficedula hypoleuca*, do not rely on their own assessment of male quality for choosing an extrapair mate, which suggests that they would use private information to choose a social partner but another source of information to select an extrapair mate. Indeed, they found that females did not engage more frequently in EPCs when they knew the quality of one potential extrapair partner compared to the females that had no information, even when their social mate was of lower quality than the extrapair male.

Despite abundant literature discussing the costs and benefits males and females incur when engaging in EPCs (Petrie & Kempenaers 1998), many questions remain regarding the mechanisms by which females assess and choose extrapair mates. I focused on one possible mechanism, mate choice copying, and developed a game-theoretic model to explore the possible roles it may play in mediating extrapair behaviours in monogamous species. Our study shows that females can adopt two different tactics that differ in their degree of selectivity to choose a social partner and then can decide whether or not to copy the decisions of others by soliciting EPCs with the already mated males. Because females can use any one tactic to choose a social partner, the benefits of mate choice copying are frequency-dependent and vary with the relative proportion of each type of female within the population, thereby justifying the use of a game-theoretic approach.

THE MODEL

All parameters of the model are listed in Table 1. I consider a monogamous breeding population with N_M males and N_F females and focus on the mating decisions of females and thus assume that males are the nondiscriminating

Table 1. Definition of the parameters used in the model

Symbol	Meaning
N_M	Number of males
N_F	Number of females
p	Proportion of selective females
$1-p$	Proportion of random females
R	Number of random females, with $R=(1-p)N_F$ or 1
S	Number of selective females, with $S=pN_F$ or 1
T	Maximum number of potential males sampled by selective females during a breeding season
x_t	Proportion of high-quality males available at time t
$1-x_t$	Proportion of low-quality males available at time t
ε	Risk of assessment error
W	Mean reproductive success of a female reproducing with a high-quality male
w	Mean reproductive success of a female reproducing with a low-quality male
N_A	Mean number of potential males sampled by selective females during a breeding season
C_A	Cost of mate assessment
C_R	Cost of male parental care reduction
R_H	Number of random females that form a pair bond with a high-quality male during the breeding season
R_L	Number of random females that form a pair bond with a low-quality male during the breeding season
$S_U(t)$	Number of selective females that are still unpaired at time t
$S_H(t)$	Number of selective females that form a pair bond with a high-quality male at time t
$S_L(t)$	Number of selective females that form a pair bond with a low-quality male at time t
$M_U(t)$	Number of males that are still unpaired at time t
y	Probability that a copier female solicits EPC with a high-quality male
$1-y$	Probability that a copier female solicits EPC with a low-quality male
$I_S(i)$	Mean reproductive success of a selective female, where i=F or C depending on whether females are faithful or copiers
$I_R(i)$	Mean reproductive success of a random female, where i=F or C depending on whether females are faithful or copiers