Deciding who to mate with: do female finches follow fashion?

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ABSTRACT

Choosing an appropriate mate is one of the most important decisions that any animal has to make. The traditional view in non-human systems is that animals are largely slaves to their genes and an individual's mate choice is handed down from their parents. However, in recent years it has become clear that many animals show active decision making in who to mate with and that females may copy mate preferences from other females in the population. In other words, females' mating decisions are affected by the current fashion in their population. Here, we explore whether "mate choice copying" occurs in a model monogamous mating system—the zebra finch. Females were given the opportunity to observe another female courting a particular type of male (we manipulated male appearance by placing small colored leg bands on each bird). In preference tests, our focal females significantly shifted their mate preferences towards the type of male that they had observed as being courted by other females. Therefore, female finches do seem to copy mate preferences, implying that there is social inheritance of information that fundamentally affects mating decisions. This is one of the first demonstrations of mate choice copying in any monogamous system and implies that many other birds may also use social

information to affect their mating decisions. We need to rethink evolutionary models of mate choice and sexual selection incorporating this form of social decision making process.

INTRODUCTION

Although selecting a mate is one of the most important decisions in an animal's life, there is surprisingly little discussion and exploration of decision making in traditional studies of mate choice (e.g., Andersson 1994; Shuster & Wade 2003; Andersson & Simmons 2006). Evolutionary studies of mate choice are dominated by gene-centered explanations of among-individual variation in mate preferences (Brooks & Endler 2001; Kokko et al. 2002; Kokko et al. 2003; Shuster & Wade 2003; Andersson & Simmons 2006), stating that mate choice is largely determined by genetically inherited factors. However, it is becoming increasingly clear that mate choice and the benefits of choosing an appropriate mate are more plastic than commonly thought, varying within-individuals as well as among-individuals (Patricelli et al. 2002; Rodriguez & Greenfield 2003; Welch 2003; Greenfield & Rodriguez 2004; Lynch et al. 2005; Lynch et al. 2006). Plasticity is the manifestation of how environmental factors increase variation (in both additive and epistatic effects) above and beyond any genetic contribution to variation in mate preferences. Even this approach to mate choice tends to ignore actual decision making processes and largely represents plasticity as either environmentally determined noise in mate preference or a correlate of changes in life stage and physiology, rather than as the result of definable cognitive process that alter mate choice.

Recently, behavioral ecologists have started to merge the individual level processes of cognitive psychology with the population level processes of evolutionary biology to explain how mate choice is affected by decision making. One example of this is the study of mate choice copying (Pruett-Jones 1992; Dugatkin 1996a; Schlupp & Ryan 1997; Brooks 1998, 1999; Freeberg et al. 1999; Galef & White 2000; Westneat et al. 2000; White & Galef 2000; Swaddle et al. 2005; Uehara et al. 2005). In mate choice copying, the choosing individual (classically females) copies the mate preferences they observe in the population and expresses this copied preference through mate choice. In other words, mate preferences are inherited through social cues that are filtered through cognitive processes (White & Galef 2000; Swaddle et al. 2005). Females view what kind of male is successful and make a decision to mate with that type of male.

Mate choice copying has been demonstrated in a handful of polygynous or lekking species, but has only recently been explored in a monogamous species (Doucet et al. 2004; Swaddle et al. 2005). It makes sense for polygynous females to copy a mate preference as it would be in a female’s interest to find quickly the few high quality males in the population. Mate choice copying promotes rapid acquisition of information that relates to mate quality. In contrast to polygynous mating systems, many males will be mated in a monogamous mating system and mate quality will be more evenly distributed across the population. Therefore, mate choice copying may not skew mating success substantially in a monogamous species and, hence, not be strongly selected for through sexual selection. However, mate choice copying could still be selected for in monogamous species where there is the opportunity to observe other mated individuals, such as in colonial breeders, and/or where the costs of developing an independent mate choice are high (Pruett-Jones 1992; Stohr 1998; White & Galef 1999). In other words, mate choice copying by monogamous females may be a cheap way of getting reliable information about male quality.

Even though we are currently unsure about the evolutionary origins or consequences of mate choice copying (Kirkpatrick & Dugatkin 1994; Laland 1994; Agrawal 2001), it is clear that animals must engage in various elements of decision making to copy mate preferences. For example, the age and sexual experience of individuals affects how females copy mate preferences (Dugatkin & Godin 1993; Ophir & Galef 2004; Amlacher & Dugatkin 2005). In addition, the information that females learn about males through mate choice copying can be generalized to new males (White & Galef 2000; Godin et al. 2005; Swaddle et al. 2005). In other words, if a hypothetical female sees males with red bills as being chosen by other females, then the copying female will be more likely to favor any male with a red bill, not just those particular individual males she saw as chosen. Hence, in some species, copying females are able to internalize copied information and make mate choice decisions dependent on the age, aggression, and sexual experience of the demonstrating female or the copied males. These are clearly cognitively complex decision making processes that push mate choice well beyond the confines of genetically inherited mate preferences.

Previously, we have shown that the monogamous zebra finch can copy mate preferences and that females can generalize information about preferred males to affect future mate preferences (Swaddle et al. 2005). This was the first convincing evidence of mate choice copying in a monogamous species (Brown & Fawcett 2005). Here, we report an experimental study further investigating how female zebra finches make decisions about mate preference and how mate choice copying is affected by social cues.

Our previous evidence for mate choice copying by female zebra finches relied on test (i.e., observer) females observing demonstrator females actually mating and starting to build nests with males for a two week period (Swaddle et al. 2005). Test females copied the preference for types of males they saw as being mated with other females. In the natural ecology of this species, archetypal copying females are probably unmated for shorter periods than two weeks (Zann 1996). Also, in other monogamous species, it is more likely that a potentially copying female would observe courtship between demonstrator females and males rather than prolonged periods of actual mating (i.e, copulations and nest building). Therefore, we investigated whether observing courtship for short bouts was sufficient to elicit mate choice copying in female zebra finches. In addition we investigated whether a known pre-existing preference for physical symmetry, manipulated by placing colored plastic leg bands on the males' legs in symmetric and asymmetric arrangements (Swaddle & Cuthill 1994a; Swaddle & Cuthill 1994b; Swaddle 1996), could be eroded by mate choice copying. In general, it is unclear how the decision making associated with mate choice copying can override or accentuate pre-existing (e.g., genetically inherited or sexually imprinted) mate preferences (Dugatkin & Godin 1992; Dugatkin 1996b).

Specifically, we examined how female zebra finches' preferences for symmetrically and asymmetrically leg banded males changed from before to after exposure to courting females and males. We predicted that females would show a general preference for symmetrically banded males before the observation period, consistent with previous studies (Swaddle & Cuthill 1994b; Swaddle 1996). We also predicted that females would increase their preference, from before to after the observation period, for males wearing the band patterns that they observed being courted by other females. In other words, we predicted that observation of conspecific courtship would be sufficient to change mate choice decisions in female zebra finches.

METHODS

Experimental subjects and general housing conditions

We used 24 virgin adult male zebra finches, 15 virgin adult test (observer) females, and eight virgin adult demonstrator females in this study. Birds were randomly selected from our outbred zebra finch colony and were either one or two generations from wild caught stock. Males and females were housed in visual but not acoustic isolation from each other in same sex group cages at approximately 20 °C. The males were housed in groups of three while the observer and demonstrator females were housed in groups of four. The birds were housed in wire cages (approximately 60 x 30 x 40 cm) and provided nutritionally complete seed and water *ad libitum*. The birds were kept on a 14:10 light:dark photoperiod under full spectrum lighting to maintain their readiness to breed (Zann 1996). None of the birds had prior experience with other individuals in the study.

The experiment was separated into three phases. First, we assessed test females' preferences for males wearing symmetric and asymmetric arrangements of red and yellow plastic leg bands. Then test females observed demonstrator females display apparent preferences for new males wearing particular arrangements of these same leg bands. Finally, we tested whether test females' altered their mate preferences in favor of males wearing the leg band arrangements that demonstrator females preferred. In other words, we tested whether test females copied preferences from the demonstrator females.

Pre-observation mate preference trials

We assessed test females' preference for males wearing three arrangements of red and yellow plastic leg bands, in a three chamber preference apparatus (Figure 1). There were three arrangements of plastic leg bands: right asymmetric, left asymmetric, and symmetric. (a) In the right asymmetric arrangement the leg bands were positioned so that males wore three units of red color and one of yellow on their right leg, while wearing three units of yellow and one of red on their left leg (Figure 2a). (b) This band arrangement was mirror reflected for the left asymmetric treatment group (Figure 2b). (c) In the symmetric leg band arrangement each male wore two units of red and two of yellow on each leg, with the red part of the bands in the center of the arrangement (Figure 2c). It is important to note that there was the same amount of red and yellow color in each band treatment group, hence reducing the effect that particular colors would have on mate preferences.

To commence a mate preference trial, a test female was placed in the preference apparatus for two hours to acclimate to the cage (Figure 1). After the acclimation period, one cage of three males was randomly selected and banded according to each of the three leg band arrangements (i.e., one wore the right asymmetric treatment, one wore the left asymmetric treatment, and one wore the symmetrically arranged bands). These three males were randomly assigned to display cages in the preference apparatus to minimize positional bias across the series of preference trials. An opaque curtain that temporarily separated the display cages from the female part of the chamber was removed so that the female could observe the display males. The female's cage was arranged so that she could view only one male at a time (Figure 1). There were opaque dividers between male display cages so that males could not visually interact with each other. During preference trials, all birds had *ad libitum* access to seed and water.

After a further 10 minute acclimation period, we videotaped (with a Sony digital video camera) all interactions among the birds for a 1-hour preference trial. We analyzed the tapes to record the amount of time a female spent performing ritualized display behaviors (short hops) in front of each male (Zann 1996; Swaddle et al. 2005). Quantification of this behavior is known to reflect actual mate choice in larger aviary cages and in the wild (Burley 1988; Swaddle & Cuthill 1994b; Swaddle 1996; Zann 1996). We used the relative amount of time a female spent displaying in front of each male as a measure of her mate preference for each leg band treatment. Each female experienced one mate preference trial and then was returned to her housing cage.

Observation trials

Observation (mate choice copying) trials were conducted in a modified preference apparatus. We placed three female demonstrator cages between the three male display cages and the larger test female observation cage (Figure 3). The demonstrator female could visually interact with only the single male she was placed in front of; she could not move into any other cages of the observation apparatus. This arrangement of cages was intended to simulate the demonstrator female displaying a preference for a particular male (i.e., the male she was placed in front of) over the other males. The test female was free to observe this female and all the males; hence, she could gain information about which male was apparently preferred over other males.

The 15 test females were randomly allocated to two groups: one that was reinforced to prefer the right-asymmetric males in observation trials ($N = 7$), and one that observed left-asymmetric males as being preferred ($N = 8$). To begin an observation trial, we randomly selected a cage of three males to serve as stimuli for the observations and banded them as before. Next we placed a randomly selected demonstrator female in the appropriate demonstrator cage (according to which type of male should appear to be preferred). Then we introduced the test female, allowed for a 10 minute acclimation period and videotaped the test female's activity for a 1-hour observation trial. These videotapes verified that test females viewed all of the males during each observation trial. Every test female experienced ten 1-hour observation trials, only nearly consecutive days. For each observation trial, females observed different males than they had experienced in the pre-observation mate preference trials. Following each observation trial, all birds were returned to their housing cages.

Post-copying mate preference test

A new set of 24 males (additional to the original 24) was used in the post-copying preference test trials so that the test females' preferences were not confounded with familiarity with particular males. We followed the same procedure as for the pre-observation mate preference trials, with display males being randomly assigned to each of the three leg band treatments (right-asymmetric, left-asymmetric, and symmetric; Figure 2) and randomly assigned to cage positions in the preference apparatus (Figure 1). Again, we analyzed the videotapes to discern test females' preferences for males wearing these leg band treatments.

Statistical analyses

All proportional preference data were arc-sine square-root transformed to improve normality. We tested for differences in the pre-observation preferences among leg band treatments using a one-way ANOVA. We compared pre-observation to post-observation leg band preferences with a paired *t*-test to determine whether test females' preferences shifted toward the band arrangement that they were reinforced to copy. All statistical tests were performed with SPSS v.13 and employed two-tailed tests of significance.

RESULTS

In the pre-observation mate preference trials, females consistently preferred the symmetrically banded males over the asymmetric males ($F_{2,42} = 3.61$, $P = 0.036$; Figure 4). This is consistent with previous data concerning general symmetry preferences among female zebra finches (Swaddle & Cuthill 1994a; Swaddle & Cuthill 1994b; Bennett et al. 1996; Swaddle 1996; Waas & Wordsworth 1999).

Test females significantly changed their mate preference from pre- to post-observation trials, with test females shifting band preferences toward the arrangement that was courted by demonstrator females in the observation trials ($t_{14} = 2.48$, $P = 0.026$; Figure 5). In other words, test females who observed an apparent preference for right-asymmetric banded males shifted their preference toward this type of male, and females who observed an apparent preference for left-asymmetric banded males increased their preference for that type of male.

CONCLUSION

Our study indicates that observations of short bouts of stereotypical courtship are sufficient to stimulate mate choice copying in female zebra finches. This is important as unmated female zebra finches are very likely to observe other courting females over several days in natural conditions. These birds breed in small colonies where fledglings mature quickly (in a matter of months) and quickly join the breeding population (Zann 1996). A young female, maturing into her first breeding attempt, will consistently be surrounded by older breeding females from which she could copy a mate preference. Therefore, our results indicate that social information could affect mate choice decision making in wild birds. At the very least, we have shown that female zebra finches' mate preference decisions are altered by information about who other females court in the local population. Females shift their preference toward the phenotype of other courted males—they follow the current fashion in mate preferences. It is also relevant that observing courtship appears sufficient to elicit mate choice copying in other species, such as quail *Coturnix coturnix* (White & Galef 1999, 2000) and the guppy *Poecilia reticulata* (Dugatkin 1996b; Amlacher & Dugatkin 2005). However, our study is the first to show that courtship is a cue which guides mate choice decisions in a monogamous species.

As test females shifted their preference toward new males who wore the same band patterns as the courted males in the observation period, we provide further evidence that female zebra finches can generalize copied preferences to new males (Swaddle et al. 2005). In a species that mates for life (i.e., a male-female pair-bond is commonly only broken by death or emigration of either partner) this is an important finding, as mating can then be skewed toward unpaired (i.e., available) males who happen to share phenotypic characters with mated (or courted) males. Potentially, this could skew mating preferences toward particular male phenotypes, therefore increasing the strength of sexual selection for those particular traits (see Figure 6). An unanswered question is whether copied preferences for male traits can also skew extra-pair mating decisions (i.e., copulations and fertilizations outside the pair-bond). Although wild zebra finches show relatively low levels of extra-pair paternity (Birkhead et al. 1990), it is still possible that social information could mediate this small degree of fitness variation—which could have an effect on evolutionary processes. We postulate that social observations of courtship and/or copulations among other conspecifics may be a significant factor in affecting extra-pair mating decisions in other species. As yet, this question is unexplored from both empirical and theoretical perspectives.

Consistent with previous studies (Swaddle & Cuthill 1994b; Swaddle 1996), female finches preferred symmetrically banded males (Figure 4). Importantly, the pre-observation symmetry preference gave us the opportunity to examine how social information can affect a pre-existing mate preference. At least in terms of leg band symmetry preferences, copying of preferences indicated by biased courtship significantly eroded a pre-existing symmetry preference. Therefore, mate choice copying could change mate choice decisions sufficiently to alter evolutionary selection pressures; thereby increasing the evolutionary significance of this form of decision making.

Our study, in general, sheds light on the evolutionary significance of the decision making associated with mate choice copying. As stated above, our results indicate that social information could skew mating preferences consistently toward particular male phenotypes. However, the pattern and strength of this change in mating skew depends on cognitive processes. If female finches decide to copy the most successful (i.e., fittest) phenotype, then the slope of mating skew could easily increase (Figure 6). An increase in mating skew would result in stronger sexual selection pressures for that male phenotype. However, if mate preferences are copied at random, or the least successful phenotypes are copied, then the slope (and sexual selection pressure) could be reduced in some scenarios (Figure 6). As, by definition, the most successful males are the ones that are most likely to provide the courtship cues that could be copied, we hypothesize that the form of copying process we have indicated here has the potential to increase the strength of sexual selection, even in a monogamous species.

However, if the copied preferences are ephemeral and are quickly forgotten, or are easily replaced with other copied preferences, then the evolutionary implications are diminished. Copied preferences have to last over at least one genetic generation to have an evolutionary effect, but last for longer for noticeable directional change. Hence, copied preferences must also likely be stored in some form of longer term memory, further emphasizing the importance of exploring the cognitive processes involved in making a mate choice decision. Outside of one study reporting that copied preference can last for 24 hours in female sailfin mollies *Poecilia latipinna* (Witte & Massmann 2003), there is very little known about the erosion and stability of copied mate preferences. Our own preliminary data from a follow-up study of female zebra finch preferences indicates that copied preferences can last for over a month and, hence, can last between consecutive nesting attempts (J. P. Swaddle, unpublished data).

At this stage in our explorations it is not clear whether mate choice copying is adaptive in zebra finches. It is possible that what we have documented in this chapter and our previous study (Swaddle et al. 2005) is a by-product of other evolved cognitive and decision making processes. For example, zebra finches show sexual imprinting at a young age (Oetting & Bischof 1996; Bischof & Rollenhagen 1999; ten Cate & Vos 1999), in other words the mate preferences and sexual displays they exhibit at maturity are affected by the social (parental) environment in which chicks are raised. Perhaps these early age processes result in the ability of mature adults to acquire information about mate preferences, but that mate choice copying itself has not been directly selected for. Mate choice copying could be a by-product of selection for sexual imprinting.

Despite how mate choice copying evolved it is clear that these small birds use socially available courtship cues to develop their mate preferences. They appear to make decisions about which males to pay attention to and, further, they generalize the appearance of these apparently preferred males and apply that information to assessing new, unpaired males. Therefore, the experimental results we report here are an important step toward showing that mate choice copying and complex decision making play important roles in establishing mate preferences in a monogamous species. To extrapolate beyond the zebra finch, it may be that this form of decision making is much more prevalent than we commonly think. The zebra finch is a classic monogamous species, with low rates of extra-pair paternity (Birkhead et al. 1990; Burley et al. 1996). In other words, this species is both socially and genetically monogamous. Mate choice copying is not expected to be common in such situations and, hence, may be even more common in other socially monogamous species that show higher levels of extra-pair paternity (genetic polygamy). This would mean that mate choice copying and social decision making could occur in many monogamous species that have the opportunity to observe courtship among other individuals in the population. We predict that complex decision making and the social inheritance of mate preferences will be discovered in many other animals, including many socially monogamous species.

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REFERENCES

Agrawal, A. A. (2001). The evolutionary consequences of mate copying on male traits. *Behavioral Ecology and Sociobiology*, *51***,** 33-40.

Amlacher, J., & Dugatkin, L. A. (2005). Preference for older over younger models during mate-choice copying in young guppies. *Ethology Ecology and Evolution*, *17***,** 161-169.

Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Andersson, M., & Simmons, L. W. (2006). Sexual selection and mate choice. *Trends in Ecology and Evolution*, *21***,** 296-302.

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C., & Maier, E. J. (1996). Ultraviolet vision and mate choice in zebra finches. *Nature*, *380***,** 433-435.

Birkhead, T. R., Burke, T., Zann, R. A., Hunter, F. M., & Krupa, A. P. (1990). Extrapair paternity and intraspecific brood parasitism in wild zebra finches, *Taeniopygia guttata*, revealed by DNA fingerprinting. *Behavioral Ecology and Sociobiology*, *27***,** 315-324.

Bischof, H.-J., & Rollenhagen, A. (1999). Behavioural and neurophysiological aspects of sexual imprinting in zebra finches. *Behavioural Brain Research*, *98***,** 267-276.

Brooks, R. (1998). The importance of mate copying and cultural inheritance of mating preferences. *Trends in Ecology and Evolution*, *13***,** 45-46.

Brooks, R. (1999). Mate choice copying in guppies: Females avoid the place where they saw courtship. *Behaviour*, *136***,** 411-421.

Brooks, R., & Endler, J. A. (2001). Female guppies agree to differ: Phenotypic and genetic variation in mate-choice behavior and the consequences for sexual selection. *Evolution*, *55***,** 1644-1655.

Brown, G. R., & Fawcett, T. W. (2005). Sexual selection: Copycat mating in birds. *Current Biology*, *15***,** R626-R628.

Burley, N. (1988). Wild zebra finches have band-colour preferences. *Animal Behaviour*, *36***,** 1235-1237.

Burley, N. T., Parker, P. G., & Lundy, K. (1996). Sexual selection and extrapair fertilization in a socially monogamous passerine, the zebra finch (*Taeniopygia guttata*). *Behavioral Ecology*, *7***,** 218-226.

Doucet, S. M., Yezerinac, S. M., & Montgomerie, R. (2004). Do female zebra finches (*Taeniopygia guttata*) copy each other's mate preferences? *Canadian Journal of Zoology*, *82***,** 1-7.

Dugatkin, L. A. (1996a). Copying and mate choice. In: Heyes, C. M., & Galef, B. G., Jr. (Eds.), *Social Learning in Animals: The Roots of Culture* (pp. 85-105). New York, NY: Academic Press.

Dugatkin, L. A. (1996b). The interface between culturally-based preferences and genetic preferences: female mate choice in *Poecilia reticulata*. *Proceedings of the National Academy of Sciences, USA*, *93***,** 2770-2773.

Dugatkin, L. A., & Godin, J. G. J. (1992). Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London B*, *249***,** 179-184.

Dugatkin, L. A., & Godin, J. G. J. (1993). Female mate choice copying in the guppy (*Poecilia reticulata*): age dependent effects. *Behavioral Ecology*, *4*, 289-292.

Freeberg, T. M., Duncan, S. D., Kast, T. L., & Enstrom, D. A. (1999). Cultural influences on female mate choice: an experimental test in cowbirds, *Molothrus ater*. *Animal Behaviour*, *57*, 421-426.

Galef, B. G., & White, D. J. (2000). Evidence of social effects on mate choice in vertebrates. *Behavioural Processes*, *51*, 167-175.

Godin, J. G. J., Herdman, E. J. E., & Dugatkin, L. A. (2005). Social influences on female mate choice in the guppy, Poecilia reticulata: generalized and repeatable trait-copying behaviour. *Animal Behaviour*, *69*, 999-1005.

Greenfield, M. D., & Rodriguez, R. L. (2004). Genotype-environment interaction and the reliability of mating signals. *Animal Behaviour*, *68*, 1461-1468.

Kirkpatrick, M., & Dugatkin, L. A. (1994). Sexual selection and the evolutionary effects of copying mate choice. *Behavioral Ecology and Sociobiology*, *34*, 443-449.

Kokko, H., Brooks, R., Jennions, M. D., & Morley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London B*, *270***,** 653-664.

Kokko, H., Brooks, R., McNamara, J. M., & Houston, A. I. (2002). The sexual selection continuum. *Proceedings of the Royal Society of London B*, *269***,** 1331-1340.

Laland, K. N. (1994). Sexual selection with a culturally transmitted mating preference. *Theoretical Population Biology*, *45***,** 1-15.

Lynch, K. S., Crews, D., Ryan, M. J., & Wilczynski, W. (2006). Hormonal state influences aspects of female mate choice in the Tungara Frog (Physalaemus pustulosus). *Hormones and Behavior*, *49***,** 450-457.

Lynch, K. S., Rand, A. S., Ryan, M. J., & Wilczynski, W. (2005). Plasticity in female mate choice associated with changing reproductive states. *Animal Behaviour*, *69***,** 689-699.

Oetting, S., & Bischof, H.-J. (1996). Sexual imprinting in female zebra finches: changes in preferences as an effect of adult experience. *Behaviour*, *133*, 387-397.

Ophir, A. G., & Galef, B. G., Jr. (2004). Sexual experience can affect use of public information in mate choice. *Animal Behaviour*, *68*, 1221-1227.

Patricelli, G. L., Uy, A. C., Walsh, G., & Borgia, G. (2002). Sexual selection: Male displays adjusted to female's response. *Nature*, *415*, 279-280.

Pruett-Jones, S. (1992). Independent versus nonindependent mate choice - do females copy each other. *American Naturalist*, *140*, 1000-1009.

Rodriguez, R. L., & Greenfield, M. D. (2003). Genetic variance and phenotypic plasticity in a component of female mate choice in an ultrasonic moth. *Evolution*, *57*, 1304-1313.

Schlupp, I., & Ryan, M. J. (1997). Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males. *Behavioral Ecology*, *8*, 104-107.

Shuster, S. M., & Wade, M. J. (2003). *Mating Systems and Strategies*. Princeton, NJ: Princeton University Press.

Stohr, S. (1998). Evolution of mate-choice copying: a dynamic model. *Animal Behaviour*, *55***,** 893-903.

Swaddle, J. P. (1996). Reproductive success and symmetry in zebra finches. *Animal Behaviour*, *51***,** 203-210.

Swaddle, J. P., Cathey, M. G., Correll, M., & Hodkinson, B. P. (2005). Socially transmitted mate preferences in a monogamous bird: a non-genetic mechanism of sexual selection. *Proceedings of the Royal Society of London B*, *272***,** 1053-1058.

Swaddle, J. P., & Cuthill, I. C. (1994a). Female zebra finches prefer males with symmetric chest plumage. *Proceedings of the Royal Society of London B*, *258***,** 267-271.

Swaddle, J. P., & Cuthill, I. C. (1994b). Preference for symmetric males by female zebra finches. *Nature*, *367***,** 165-166.

ten Cate, C., & Vos, D. R. (1999). Sexual imprinting and evolutionary processes in birds: a reassessment. *Advances in the Study of Behavior*, *28***,** 1-31.

Uehara, T., Yokomizo, H., & Iwasa, Y. (2005). Mate-choice copying as Bayesian decision making. *American Naturalist*, *165***,** 403-410.

Waas, J. R., & Wordsworth, A. F. (1999). Female zebra finches prefer symmetrically banded males, but only during interactive mate choice tests. *Animal Behaviour*, *57***,** 1113-1119.

Welch, A. M. (2003). Genetic benefits of a female mating preference in gray tree frogs are context-dependent. *Evolution*, *57***,** 883-893.

Westneat, D. F., Walters, A., McCarthy, T. M., Hatch, M. I., & Hein, W. K. (2000). Alternative mechanisms of nonindependent mate choice. *Animal Behaviour*, *59***,** 467-476.

White, D. J., & Galef, B. G., Jr. (1999). Mate choice copying and conspecific cueing in Japanese quail, *Coturnix coturnix japonica*. *Animal Behaviour*, *57***,** 465-473.

White, D. J., & Galef, B. G., Jr. (2000). 'Culture' in quail: social influences on mate choices of female *Coturnix japonica*. *Animal Behaviour*, *59***,** 975-979.

Witte, K., & Massmann, R. (2003). Female saiflin mollies, *Poecilia latipinna*, remember males and copy the choice of others after 1 day. *Animal Behaviour*, *65***,** 1151-1159.

Zann, R. A. (1996). *The Zebra Finch: A Synthesis of Field and Laboratory Studies*. Oxford, UK: Oxford University Press.

Figure legends

Figure 1. Plan view of the mate preference apparatus. Each of the stimulus males were placed in a small cage, separated by opaque barriers (gray bars). The test female was placed in a long chamber so she could observe each of the stimulus males. Each observation compartment was separated with an opaque barrier so that a female could see only one male at a time. There were abundant perches throughout all the cages. We used the proportion of time females spent displaying in the compartment immediately in front of each male as an index of female preference. All birds had *ad libitum* access to food and water throughout trials.

Figure 2. Cartoon representations of the three colored plastic leg band arrangements used for this study: (a) the right-asymmetric; (b) left-asymmetric; and (c) symmetric band treatments. These small plastic leg bands were easily removed and replaced on birds between trials.

Figure 3. Plan view of the test observation chamber. Each of the stimulus males were placed in a small cage, separated by opaque barriers (gray bars), as in Figure 1. A demonstrator female was placed in one of three small cages in front of each of the stimulus males. A demonstrator female could see only one stimulus male. The test (observing) female was placed in a long chamber so she could see each of the stimulus males (one at a time) and also see the demonstrator female courting one of these stimulus males. The position of the

demonstrator female changed between trials (see Methods section for more details). Here we have illustrated an example where the demonstrator female is placed in the middle cage. All birds had *ad libitum* access to food and water throughout trials.

Figure 4. Mean (± s.e.m.) preference for leg band arrangements in the pre-observation mate preference trials. Before observation trials, females had a general preference for males wearing the symmetric band arrangement.

Figure 5. Mean (± s.e.m.) preference for males wearing the reinforced (i.e., courted by another female in the observation trials) leg band arrangement in the pre- and post-observation trials. Females significantly increased their preference for novel males wearing the reinforced band arrangement (whether that was the left- or the right-asymmetric band treatment) indicating that they copied apparent mate preferences displayed in the observation trials.

Figure 6. Hypothetical mating skew in (a) polygynous and (b) monogamous mating systems. In the polygynous situation a small number of males get most of the matings. In the monogamous mating system most males will get a mate in any one breeding season; hence, the slope of mating skew is much more shallow than in the polygynous situation. The slope of the mating skew curve indicates the strength of sexual selection acting on males. In the monogamous situation, if mate choice copying shifts mating toward the already successful males, the

mating skew and strength of sexual selection can increase, as indicated by line (c) on the graph. However, if mate choice copying favors the least successful males, the mating skew could become flatter and sexual selection weaker, as indicated by line (d) on the graph. Therefore, this simple model can help visualize the outcome of decision making on the strength of sexual selection in a monogamous mating system where mate choice copying occurs.

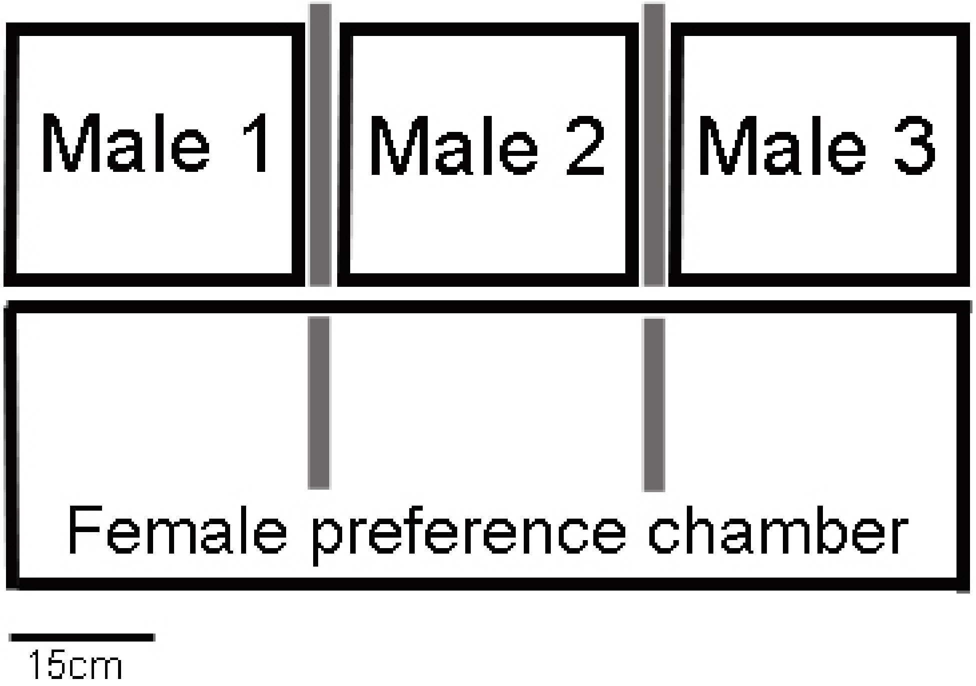
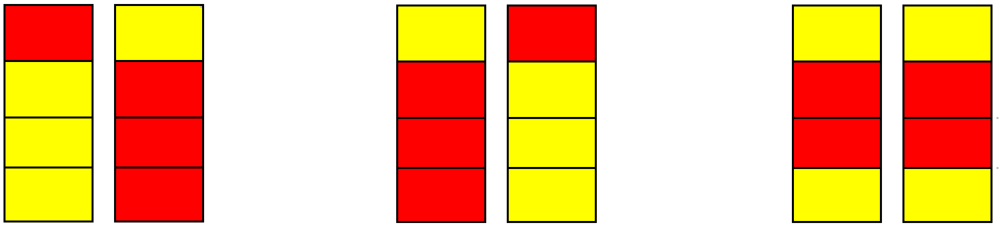


Figure 1

Swaddle & Clelland



(a) Right-asymmetric (b) Left-asymmetric (c) Symmetric

Figure 2

Swaddle & Clelland

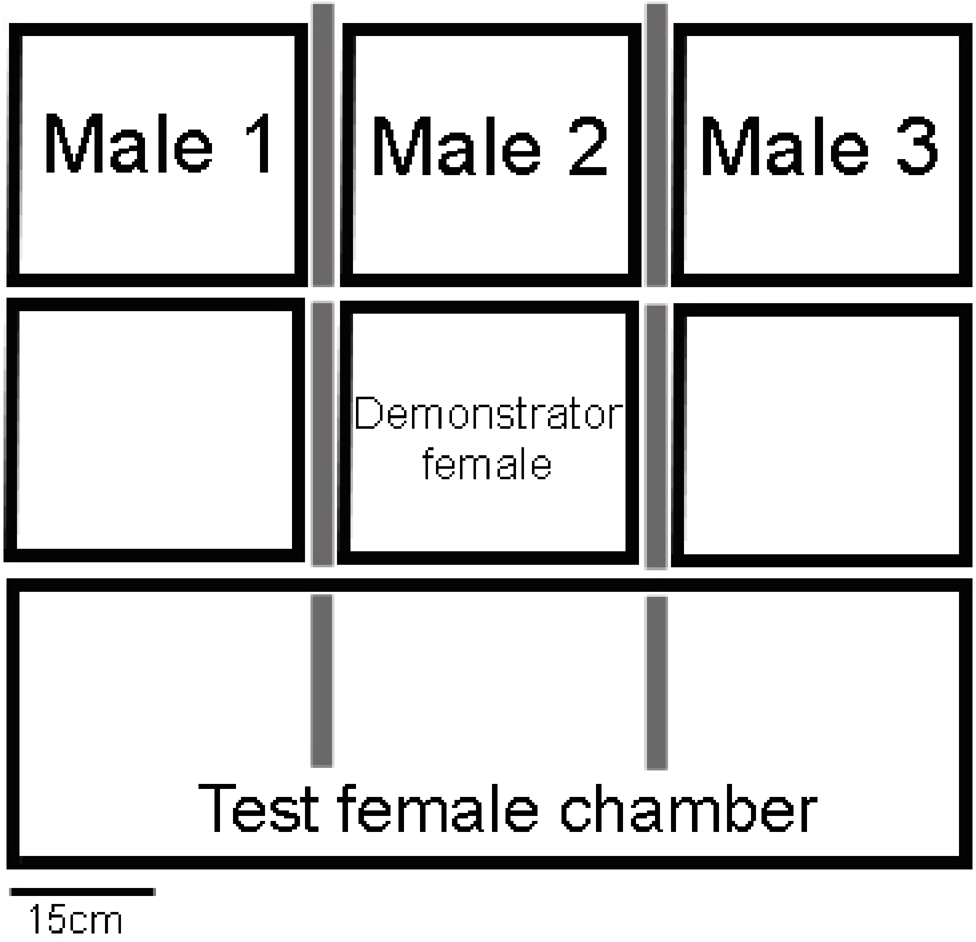


Figure 3

Swaddle & Clelland

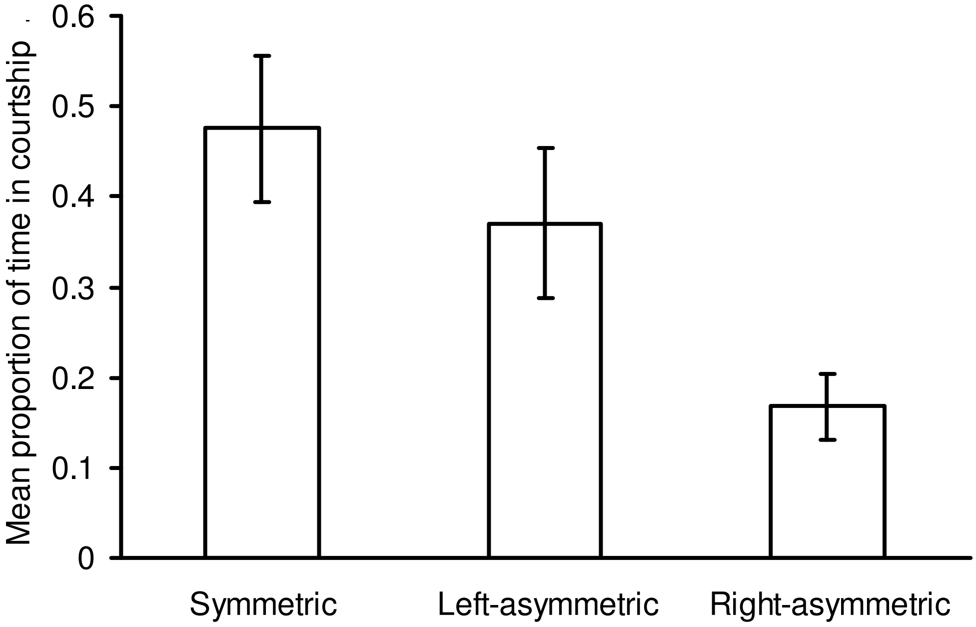


Figure 4

Swaddle & Clelland

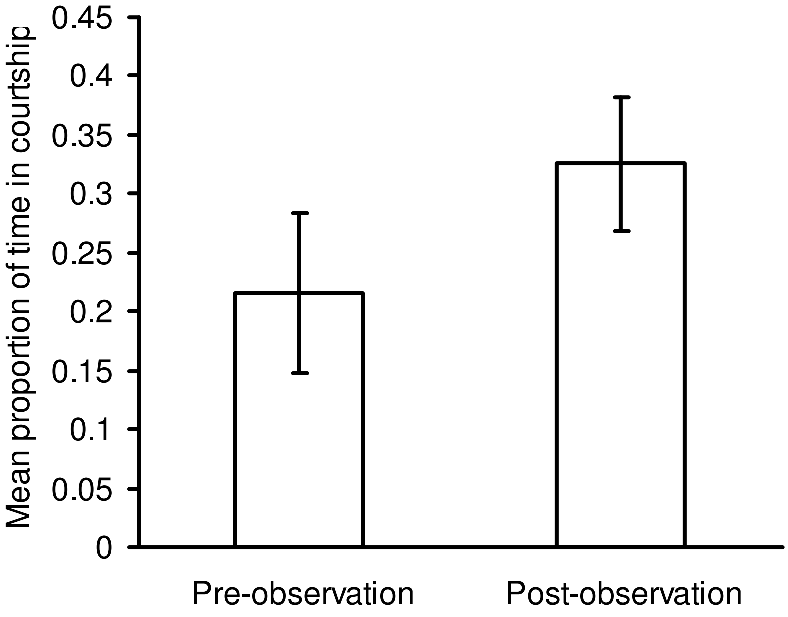


Figure 5

Swaddle & Clelland

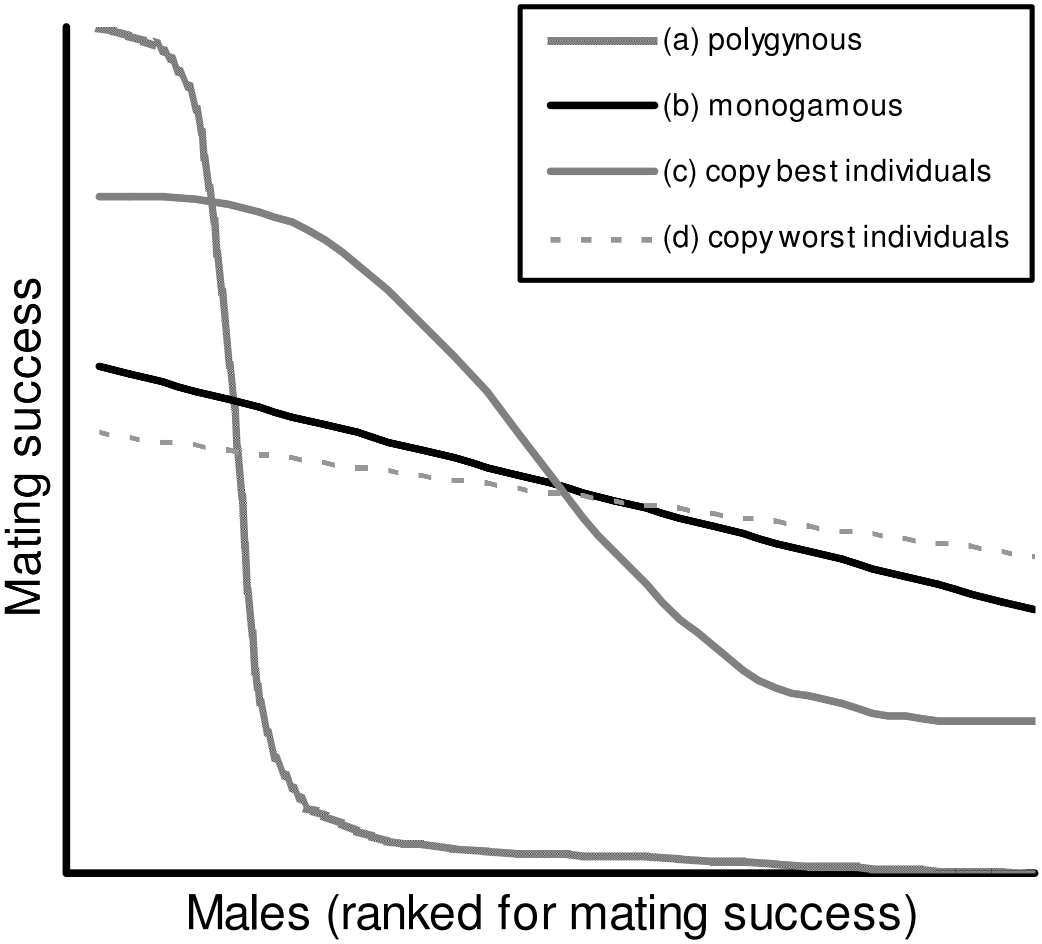


Figure 6

Swaddle & Clelland