Socially transmitted mate preferences in a monogamous bird: a non-genetic mechanism of sexual selection

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There is increasing evidence that animals can acquire mate preferences through the use of public information, notably by observing (and copying) the mate preferences of others in the population. If females acquire preferences through social mechanisms, sexual selection could act very rapidly to spread the preference and drive elaboration of the preferred trait(s). Although there are reports of 'mate-choice copying' in polygynous species, there is no clear evidence for this process in monogamous species. Here, we investigated whether adult female zebra finches *Taeniopygia guttata* can socially acquire sexual preferences for individual males and, in a separate study, for a generalized trait (coloured leg bands) of males. In both studies, test females observed males in two simultaneous conditions: a ('chosen') mixed-sex situation in which a male was paired with a (model) female, and a ('unchosen') same-sex situation in which a male was paired with another male. In the first experiment, after two weeks of females observing males, test females significantly preferred individual males who had been paired with another female (i.e. chosen males). In the second experiment, test females significantly preferred novel males that were wearing the same leg band colour as the apparently chosen males. Our findings are consistent with the conclusion that female zebra finches' mate preferences are altered by public information. Our study implies that mate preferences can spread rapidly through populations by social mechanisms, affecting the strength of sexual selection in a monogamous species.

Keywords: mate-choice copying; public information; sexual selection; zebra finch; *Taeniopygia guttata*

1. INTRODUCTION

Most models of sexual selection assume that individuals in a population show independent mate choice (review in Andersson 1994). However, it is becoming increasingly clear that mate preferences can be shaped by publicly available information, and can often be non-independent (Dugatkin 1992; Pruett-Jones 1992; Höglund *et al*. 1995; Grant & Green 1996; Schlupp & Ryan 1997; White & Galef 1999; Westneat *et al*. 2000; Danchin *et al*. 2004; Ophir & Galef 2004; Qvarnström *et al*. 2004). There are many mechanisms by which females could acquire a mate preference through social processes resulting in non-independent mate choice (Westneat *et al*. 2000).

In terms of population changes, non-independent mate choice can lead to faster spread of preferences through social mechanisms than genetic mechanisms (Kirkpatrick & Dugatkin 1994; Freeberg 2000; Agrawal 2001; Danchin *et al*. 2004). A fast spread of preferences can lead to rapid evolution of display characters, as long as the non-independent preferences are transmitted intact across many generations (Brooks 1996). The use of publicly available information in social transmission of a mate choice may also minimize mate searching and mate sampling costs, which has important implications for sexual selection processes (see predictions in Kokko *et al*. 2002).

In terms of individual fitness, non-independent mate choice can lead to rapid acquisition of a mating preference for high-fitness males, and so enhance reproductive output (Stohr 1998). Non-independent mate choice has also been described as a successful female strategy that ensures a female's offspring inherit alleles similar to the rest of the population, so the offspring will not be uncompetitive (Sirot 2001). Therefore, demonstrating cases of non-independent mate choice and the use of public information in shaping mate preferences is important to understanding how sexual selection can shape evolutionary processes and secondary sexual trait design (Agrawal 2001; Danchin *et al*. 2004).

Of the many mechanisms suggested to explain non-independent mate choice, much of the research effort has been focused on social transferral of a preference for particular individuals—'association to male' (Westneat *et al*. 2000). In several cases, non-independent mate choice for particular individuals has been demonstrated (e.g. Dugatkin 1992, 1996; Höglund *et al*. 1995; Briggs *et al*. 1996; Grant & Green 1996; Schlupp & Ryan 1997; Galef & White 1998; White & Galef 1999; Witte & Ryan 2002; Ophir & Galef 2004). But, in other cases, it seems that females are more likely to show independent mate choice (e.g. Clutton-Brock & McComb 1993; Brooks 1996; Fiske *et al*. 1996; Patriquin-Meldrum & Godin 1998; Slagsvold & Viljugrein 1999).

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One mechanism of non-independent choice that has received relatively little attention, but has significant implications for models of sexual selection (Kirkpatrick & Dugatkin 1994; Laland 1994), is preference based upon traits of model individuals (White & Galef 2000). If females acquire preferences that are based on general trait features of males they observe as chosen, then mating success will not be increased in particular individuals but in any bearers of the favoured traits in the population. This situation is more akin to how we view trait evolution in sexual-selection models of independent mate choice (Andersson 1994). Selection will act in favour of the trait *per se*. To our knowledge, trait-specific social preferences have been demonstrated on only one previous occasion. Female Japanese quail *Coturnix japonica* can acquire general preferences for traits (artificial colour patches and pseudomutant white crest feathers) by observing males that possess these traits engaging in sexual behaviours. This finding has been interpreted as a demonstration of 'cultural' inheritance of trait preference and, obviously, has significant implications for the ways in which sexual selection operates in quail (Brooks 1998; White & Galef 2000). A recent field study indicated a similar phenomenon may occur in collared flycatchers (*Ficedula albicollis*). However, it was not clear in the latter study whether females were developing preferences for individual males with a novel trait or the novel trait *per se* (Qvarnström *et al.* 2004).

To date, most empirical evidence of non-independent mate choice (also referred to as 'mate-choice copying') has been limited to polygynous and lekking species (e.g. Dugatkin 1996; Schlupp & Ryan 1997; Galef & White 1998; Patriquin-Meldrum & Godin 1998; White & Galef 1999, 2000; Westneat *et al.* 2000; Ophir & Galef 2004). Here, we investigated whether individual-based and trait-associated non-independent mate choice occurs in the monogamous zebra finch *Taeniopygia guttata*. Specifically, we studied the propensity of adult female zebra finches to socially acquire preferences for particular individual males that were observed to be successful mates (cf. Doucet *et al.* 2004). In a second study, we also investigated the change in females' preferences for a generalized trait (leg band colours) of males they observed as being successful mates. Previous experiments have clearly demonstrated that leg band colour influences mate choice in zebra finches (Burley *et al.* 1982; Burley 1986, 1988; Zann 1994) and that the behaviour of individuals wearing colour bands influences the social learning of other finches that are observing them (Benksin *et al.* 2002). If public information is important, and mate-choice copying occurs in this species, we predicted that females would acquire a preference for individual males and for the generalized traits (i.e. band colour) of males they observed in sexual association with another female.

2. METHODS

We used virgin wild-type adult zebra finches in this study in which males and females had no prior experience of each other. All birds were kept on 14 : 10 h light : dark photoperiod at a constant temperature of approximately 20 °C and with *ad libitum* access to seed and water. Lighting was provided by ceiling-mounted fluorescent tubes.

(a) Experiment 1: copying of preferences for individual males

Twenty female zebra finches were housed singly in wire cages (approximately $30 \times 20 \times 40$ cm). The test females' housing cage was placed between two male stimulus cages (approximately $30 \times 20 \times 40$ cm). In the 'mixed-sex' stimulus cage, a male was paired with another adult female zebra finch. In the 'same-sex' stimulus cage, a male was paired with another adult male zebra finch. Therefore, each test female observed adult males in two conditions: a mixed-sex (apparently successfully chosen) and a same-sex (apparently unchosen) housing condition. Each test female could only see their particular stimulus birds, although they were not acoustically isolated from the other birds in the room. We chose to use a same-sex pair of males, rather than a lone male as the alternative stimulus to the mixed-sex male–female pair, to control for the number of birds associated with each treatment. Zebra finches are highly social and are known to aggregate in large flocks and groups (Zann 1996). Therefore, social group size was an important factor to de-confound from our experimental treatment groups.

We examined test females' preferences for the mixed-sex and same-sex males in a two-chamber choice apparatus one week and two weeks into the observation period. We did not assess females' preferences for the stimulus males before the observation period, as females could have acquired a preference for a particular male during this test trial (i.e. before males were assigned to mixed-sex or same-sex conditions) that endured during the remainder of the experiment (Zann 1996; Doucet *et al.* 2004), masking effects of social housing and public information on mate preferences for individual males.

The choice chamber was a long cage (approximately $60 \times 30 \times 40$ cm) in which there were two pairs of wooden perches at each end, from which females showed ritualized display hopping in front of a male (figure 1). There were two perches in the centre of the choice chamber, located next to food and water. For each test female, we placed her mixed-sex stimulus male in one of the end cages (randomly determined either left or right) and her same-sex stimulus male in the other (figure 1). The test female was released into the central cage so she could see both males and could choose to associate with either.

Each mate preference trial lasted for 80 min. After 40 min, the relative positions of the two males were switched to control for any side bias in the choice chamber. We recorded all behaviours during the trial using a Sony digital video camera. Following a 10 min settling down period, we quantified the amount of time females spent in courtship activity in front of each of the males. When the male cages were switched after 40 min, we allowed the female to settle down for another period of 10 min before continuing data collection. Hence, we recorded mate preference for a total of 60 min per test female.

We defined female courtship activity as the time she spent displaying on the closest perch to the male and excluded times when the female was sleeping, preening, immobile or facing away from the male. Time spent on any other perch in the choice chamber did not count as courtship activity. Time spent displaying closest to a male successfully quantifies mate preferences in zebra finches and has been demonstrated to relate to real mate choice on several occasions (e.g. Swaddle & Cuthill 1994; Swaddle 1996; Zann 1996).
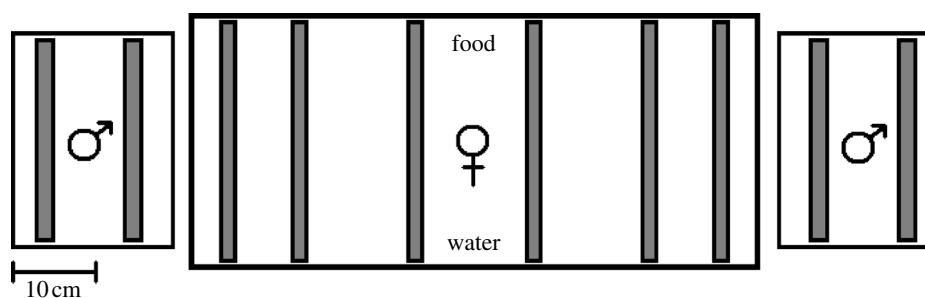
Figure 1. Plan view of the choice chamber used in both experiments. Females were placed in the central chamber and could see both males in the end cages from every part of the chamber. Females had access to food and water in the centre of their cage. Dark bars indicate perches.

(b) *Experiment 2: copying of band-colour preferences*

In the second experiment, 22 virgin test adult females (different individuals to the first experiment) were housed in identical observation cages in which they could observe a mixed-sex stimulus male (as described previously) in one cage and a same-sex stimulus male in the other. The arrangement of the male stimulus cages differed slightly from those in the first experiment in that the cages were larger (approximately $60 \times 30 \times 40$ cm) and had a wooden nest-box in one corner with nesting material. We assigned two white plastic leg bands (one on each leg) to half of the mixed-sex males ($n = 11$), while the same-sex males wore orange bands. In the remaining cages ($n = 11$), mixed-sex males wore orange, and same-sex males wore white, leg bands. Bands were 'finch' size and obtained from L&M Bird Leg Bands Incorporated, California.

Before the (mate-choice copying) observation period began, we tested whether test females had a pre-existing preference for either of the leg band colours we used in this experiment (i.e. white versus orange bands). We conducted a single mate preference trial with each test female, using the same general protocol as for experiment 1, except the preferences trials lasted for 60 min instead of 80 min. For each mate preference trial, two unfamiliar males were placed in the single cages at either end of the long mate-choice chamber (see figure 1). One male wore two white plastic leg bands (one on each leg); the other male wore two orange plastic leg bands. It is important to remark that the choice males were different individuals to the mixed-sex and same-sex stimulus males.

Following this initial colour-band preference trial, test females were placed in their observation cages for two weeks (as described above). During this time we observed nest-building and courtship behaviours between the male and female in all of the mixed-sex stimulus cages. After two weeks of observations, we again examined test female band preferences. We used the same protocol as in the previous test, and new (unfamiliar) males were used as the choice males in the second preference test.

All of the animal procedures were approved by our Institutional Animal Care and Use Committee and followed federal guidelines for animal welfare.

(c) *Statistical analyses*

As our measure of preference was calculated as a ratio of time spent in the two ends of the choice chamber, we square-root transformed all ratio raw data so that the data did not deviate significantly from the symmetric frequency distribution assumption of t-tests. In experiment 1, test female preference for males in the choice chamber was assessed with a paired t-test. We analysed the change in relative preference for the predicted male (i.e. the mixed-sex stimulus male) from week one to week two with a paired t-test. Similarly, in experiment 2, band-colour preferences before observations were assessed using paired t-tests, as were preferences for mixed-sex versus same-sex male band colours two weeks after observations. In addition, we analysed the change in relative preference for the predicted band colour (i.e. the white band if the female's mixed-sex stimulus male wore white leg bands, and vice versa) with a paired t-test where extent of preference 'before' the observations is compared with extent of preference 'after'. All statistical tests were conducted using SPSS 11 for Windows, employing two-tailed tests of probability.

3. RESULTS

(a) *Experiment 1: copying of preferences for individual males*

Choice tests after one week of social observations indicated no significant preference for the mixed-sex over the same-sex male (paired t-test of square-root-transformed proportion of time spent displaying in front of mixed-sex stimulus males versus same-sex stimulus males, $t_{19} = 0.076$, $p = 0.941$). However, after two weeks of observation, there was a significant preference for the mixed-sex males ($t_{19} = 2.81$, $p = 0.011$; table 1). After two weeks of observations, test females developed a preference for males that were associated with another female However, the within-female shift in preference for the mixed-sex male from the first week to the second week of the observations was not quite significant, but in the predicted direction ($t_{19} = 1.92$, $p = 0.071$).

(b) *Experiment 2: copying of band-colour preferences*

Prior to the observation period, females did not exhibit a preference for males wearing orange versus white leg bands ($t_{21} = 0.009$, $p = 0.993$). This is consistent with previous studies (Zann 1996). However, after two weeks of observations, test females had developed a preference for the leg band colour worn by the mixed-sex stimulus males ($t_{21} = 2.34$, $p = 0.029$; table 1). Individual females significantly changed their mate preference towards the predicted band colour (i.e. towards the band colour of the mixed-sex stimulus males; paired t-test of square-root-transformed within-individual change in proportion of time spent displaying in front of males wearing mixed-sex band colours from week zero to week two: $t_{21} = 2.22$, $p = 0.038$).

Table 1. Mean ($\pm$s.e.m.) proportion of time spent by test females in courtship display behaviour in front of males from experiment 1 (copying of preference for an individual male) and experiment 2 (copying of preference for a generalized male traits).

(In experiment 1, females chose between males from the mixed-sex and same-sex observation cages, following two weeks of social observation. In experiment 2, females chose between males wearing leg band colours associated with mixed-sex and same-sex-stimulus males, after two weeks of observations. Refer to text for further details of each experiment.)

	mixed-sex	same-sex
experiment 1 (preference for individual males)	0.654 ($\pm$0.055)	0.346 ($\pm$0.055)
experiment 2 (preference for leg band colours)	0.633 ($\pm$0.056)	0.367 ($\pm$0.056)

4. DISCUSSION

Adult female zebra finches appear to develop sexual preferences for specific males and the generalized traits of males through the use of publicly available information. As far as we are aware, this study is the first to report such an effect, which is consistent with non-independent mate choice (i.e. mate-choice copying), in a monogamous species. Another recent study reported that public information affects female zebra finch courtship behaviour, but did not find conclusive evidence for mate-choice copying (Doucet et al. 2004). Hence, we propose that there is growing evidence that public information affects mating preferences in this monogamous species.

Our first experiment indicates that unpaired female zebra finches can socially acquire preferences for particular males that are associated with another female (rather than a male), potentially skewing mating success towards apparently successful males. Specifically, after two weeks of observation, females preferred males that they observed in association with another female. Although the within-individual change in females' preferences for these males from the first to the second week of observations was not quite significant ($p=0.071$), the patterns are consistent with a shift in female preference towards the apparently successful males.

We cannot discriminate what cues affect this apparent shift in mate preferences. It may be that behavioural differences between males associated with a female versus males housed in single sex groups could influence the shift in mate preferences. However, none of the birds in our study exhibited the consequences of overt aggressive or dominance encounters (e.g. feather plucking). Hence we cannot conclude that males in the mixed-sex cages were either more dominant or differently aggressive to males in the same-sex cages. Aggression is known to affect socially acquired mate preferences in quail *Coturnix coturnix* (Ophir & Galef 2004). However, it is prudent to point out that there may be behavioural differences, associated with housing conditions, which could be driving the patterns in our data, and not the apparent mating status *per se* of the stimulus birds. We require further experimentation to understand the exact behavioural mechanisms underlying the shift in female preferences.

Nonetheless, males associated with females appeared to be preferred. What does this mean for the natural mating system and strength of sexual selection in zebra finches? Rates of extra-pair fertilizations in zebra finches are low (commonly less than 5%; Zann 1996), implying that already-paired males may not have the capacity to substantially increase their mating success. However, zebra finches may switch partners from one breeding attempt to another, and they can have more than one breeding attempt within a season (Zann 1996). It may be advantageous for a previously unpaired female to attempt to pair with a previously successful male in a subsequent breeding attempt. Therefore, female copying of preferences for a particular male may be selected for in natural populations. In addition, if unpaired females can socially acquire preferences for traits of successful males (Westneat et al. 2000; White & Galef 2000), unpaired males displaying the preferred traits will experience increased mating success. Therefore, mating success could be substantially altered across a population, increasing the strength of sexual selection. The second experiment provides further support for the notion that female zebra finches can socially acquire preferences for traits of apparently chosen males. However, even in the second experiment, we cannot identify the precise cues (e.g. behavioural differences between the mixed-sex and same-sex males) that are driving the shift in mate preferences. No matter which precise mechanism applies, it is important to stress that females relied on mating performance (i.e. public information) to develop their mate preferences.

It is also important to remark that our females did not actually observe the mate-choice process of another female. They observed the outcome of an 'apparent' choice, i.e. a pair-bonded situation. Therefore, it seems that female zebra finches do not need to observe the actual choice behaviour to socially acquire the mate preference of the model individual. Females in the wild could be more likely to see pair-bonded males and females than active choice behaviour because prolonged periods of choice behaviours are less likely to be performed in open environments, owing to the increased predation risk of such behaviours (Jennions & Petrie 1997; Kokko et al. 2002). Therefore, our study has relevance to natural forms of stimulation related to potential social acquisition of mate choice.

In both the experiments reported here, two weeks of social observations influenced female preferences. Compared with previous studies, two weeks is a long time. For example, mate preferences can be affected by 10 min of observation in polygynous quail (White & Galef 1999, 2000). A previous investigation of whether female zebra finches' preferences for particular males are reversed by the influence of public information failed to support the mate-choice copying hypothesis (Doucet et al. 2004). However, females in that study observed stimulus males for a short learning period (30 min). Our experiments indicate that it may take more than one week of social observations to alter female zebra finch preferences. It is likely that in wild populations of zebra finches, unpaired females interact with pair-bonded males, as nests of this opportunistic breeder are commonly less than 20 m apart (Zann 1996). Males usually assist in nest building, which takes one to two weeks. It is possible that unpaired females

observe such activities and develop preferences for males (or traits of males) that successfully contribute direct nest-building benefits to females. Hence, we hypothesize that by acquiring preferences for traits of males that remain around a nest and female for more than one week, females could be selecting for direct mating benefits (i.e. assistance in nest construction). It is also possible that the observed preference 'copying' is a by-product of other social mechanisms. For example, the mating preferences of zebra finches can be influenced by early life visual experiences, i.e. they exhibit sexual imprinting (ten Cate & Vos 1999; Witte & Sawka 2003), and imprinted preferences are known to change in adulthood through social processes (Oetting & Bischof 1996). Perhaps the effect of the adult social environment on mate preferences is a by-product of sexual-imprinting mechanisms.

Whichever interpretation applies, showing that mate preferences of a monogamous species can be altered by public information in mature adults is an important extension of current sexual-selection theory. Mate preferences can be spread horizontally (and obliquely among unrelated individuals) through adult populations, potentially influencing the strength of sexual selection on both the preference and the preferred traits in a monogamous species (Kirkpatrick & Dugatkin 1994; Laland 1994; Westneat *et al*. 2000; Sirot 2001; Danchin *et al*. 2004). Additionally, as social conditions can affect female preference, it is clear that female preference is not a static, invariable trait in this species. Sexual-selection theory often treats female preference as a relatively invariable trait, though recent evidence indicates that female preferences can vary with life stage, and may lead to the evolution and maintenance of multiple male ornaments (Coleman *et al*. 2004). It may be relevant that male zebra finches also possess multiple sexual ornaments.

As a caveat to this study, it has previously been shown that social acquisition of mate choice does not necessarily override independent mate choice based on evolved attractive characteristics. For example, mate-choice copying does not supersede the normal situation of females preferring males of larger body size in the sailfin molly *Poecilia latipinna* (Witte & Ryan 1998). However, when the observation (copying) time was increased, significant mate-choice copying was observed (Witte & Noltemeier 2002). This latter study further indicates that a longer observation period increases the probability of mate-choice copying. In zebra finches, preference for a particular male is not reversed by a brief bout of social observations (Doucet *et al*. 2004). In the case of our study, if we had used band colours of known varying attractiveness (e.g. red versus light green bands) it would have been simple for females to discriminate attractive from less attractive males and so reduce the likelihood of copying behaviours (Nordell & Valone 1998; Stohr 1998). Evolutionary models explicitly predict that females should be more likely to socially acquire mate preferences when the pool of available mates does not seem to vary greatly in attractiveness (Sirot 2001). It would be interesting, and relevant, to explore the strength of mate-choice copying when the preference is based on features that are variable and known to affect attractiveness. Essentially, there is a need to compare the relative strength of independent and non-independent mate choice (Danchin *et al*. 2004).

Here, we have indicated that non-independent mate choice could be strong, even in this monogamous species.

In general, we propose that public information can play an important role in shaping sexual-selection mechanisms, even in a monogamous species. Social transmission of mate preferences may be more widespread than accounted for in current sexual-selection models (Andersson 1994; Kokko *et al*. 2002), further emphasizing that sexual selection can be a potent evolutionary force (Shuster & Wade 2003), potentially driving rapid evolution of ornamentation and behaviours.

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