

Original Article

# Novel mate preference through mate-choice copying in zebra finches: sexes differ

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The development of preferences for males with sexual ornaments is still not well understood. Therefore, we investigated whether the use of public information in mate-choice copying can explain the development of mate preferences for a novel phenotype in male and female zebra finches (*Taeniopygia guttata castanotis*). In a binary choice situation, birds could choose between 2 conspecifics of the opposite sex of 2 different phenotypes: an unadorned phenotype and an adorned phenotype with a red feather on the forehead, simulating the novel phenotype. When no public information was provided, females and males spent a similar amount of time in front of individuals of both phenotypes. After observing a single, unadorned individual and a pair with 1 adorned partner for 2 h, females and males could choose between other individuals of both phenotypes in 2 consecutive mate-choice tests. Females spent significantly more time in front of males of the adorned phenotype after the observation period than before the observation period. This shows that females copied and generalized the mate choice of other females for males of the new phenotype. In contrast to females, males did not copy the mate choice of other males. Results from controls provided no alternative explanation for the change in mate choice in females. Our study shows that sexes differ in using public information in mate-choice decisions and that mate-choice copying is a meaningful mechanism for the cultural inheritance of mate preferences in female zebra finches.

**Key words:** artificial ornamentation, development of mate preferences, mate-choice copying, novel traits, public information, zebra finch.

## INTRODUCTION

Theories of intersexual selection provide different explanations for the existence and maintenance of mate preferences in a species and of traits formed by sexual selection (Fisher 1930; Zahavi 1997; van Doorn et al. 2009; Maan and Seehausen 2011). The development of mate preferences for sexual traits and how these traits can arise (Pfennig et al. 2010; Ruell et al. 2013) and spread within a population or species, however, are still debated (Kokko et al. 2003; Arnqvist 2006).

Although most models and theories in sexual selection predict that male and female mate preferences are genetically based (Bakker and Pomiankowski 1995; Iwasa and Pomiankowski 1999; Mead and Arnold 2004), there is increasing evidence that nongenetic factors can have a strong impact on developing mate preferences and therefore the spread of novel traits within a population. Especially for individuals living in groups, the social environment provides the opportunity for interactions between and observations of conspecifics and thus the use of public information (sensu Danchin et al. 2004; Dall et al. 2005; Nöbel and Witte 2011). One

form of using public information in the context of mate choice is mate-choice copying (Westneat et al. 2000; Witte 2006a). It is defined as a nonindependent mate choice in which a female's probability of choosing/rejecting a given male or phenotype increases if other females have previously chosen/rejected that male (Pruett-Jones 1992; Witte and Ueding 2003), and the same is true for males.

Mate-choice copying has been experimentally demonstrated in several fish species (overview in Nöbel and Witte 2011). It was also shown in mammals (Galef et al. 2008; Bowers et al. 2012), *Drosophila* (Mery et al. 2009; Loyau et al. 2012; but see Auld et al. 2009), and several bird species (Gibson et al. 1991; Höglund et al. 1995; White and Galef 2000), including female zebra finches (Swaddle et al. 2005; Drullion and Dubois 2008; but see Doucet et al. 2004). The influence of public information on female mate choice can be so strong that socially acquired information can overwrite genetically based preferences for certain male phenotypes in females (e.g., Dugatkin 1996, 1998; Witte and Noltemeier 2002). Females not only copy the choice for individual males but they also maintain the socially learned preference, generalize, and prefer males of the same phenotype as the observed preferred males (Witte and Noltemeier 2002; Godin et al. 2005). Thus, the prerequisites for cultural inheritance of a socially driven mate choice are fulfilled (Brooks 1998). This is also true for male mate-choice

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copying. If males generalize between individuals based on the female phenotype instead of copying the choice for an individual female, then sperm competition is not higher in copying males than in males choosing independently.

To investigate whether mate-choice copying can support the development of a preference for mates bearing a novel trait, we used the zebra finch as a model species. The zebra finch (*Taeniopygia guttata castanotis*) is a socially monogamous species with biparental brood care. Due to the fact that both males and females highly invest in offspring, both sexes are choosy. Many studies with zebra finches have shown that both sexes choose among potential mating partners (e. g. Swaddle and Cuthill 1994; DeKogel and Prijs 1996; Jones et al. 2001; Forstmeier and Birkhead 2004; Simons and Verhulst 2011) and they are even influenced by artificial ornamentation in their choice (e.g., Burley et al. 1982; Swaddle et al. 2005; Witte and Caspers 2006; Drullion and Dubois 2008). Zebra finches live in large flocks throughout the whole year (Zann 1996), which provides a good opportunity to observe conspecifics and copy each others' mate-choice decisions.

So far, there are only 2 experimental studies showing that zebra finch females copy the mate choice of other females (Swaddle et al. 2005; Drullion and Dubois 2008; but see Doucet et al. 2004). Swaddle et al. (2005) have shown that female zebra finches preferred individual males, and also males of the same phenotype (same leg band color) as mates apparently chosen by other females, after 2 weeks of observation. In nature, however, females will not have as long to find a mate. Drullion and Dubois (2008) have shown that an observation period of 1 h is sufficient to copy the mate choice of conspecific females. Therefore, we tested whether male and female zebra finches use public information in mate choice, that is, whether both sexes copy the mate choice of others by copying a preference for a novel artificial phenotype. To our knowledge, there is currently no published data on mate-choice copying in male zebra finches. For our experiments, we created a novel phenotype by adorning males and females with a red feather on the forehead. Zebra finches lack an exaggerated crest, as do other estrildid finches (Wolters 1979–1982; Goodwin 1982). Therefore, we considered the red feather to be a novel adornment in the zebra finch.

We conducted mate-choice copying experiments with both males and females. Additionally, we conducted 4 controls to test for alternative explanations. In the first control, we tested whether females would choose consistently when they had no opportunity to copy. In the second control, we tested whether social attractiveness and/or local enhancement (Heyes et al. 2000) might be responsible for any change in mate choice. Here, we presented 2 females versus 1 female to test whether a presentation of 2 birds was the reason for a possible change in mate choice, excluding sexual motivation

by using only female birds. In the third control (2 versions: one for each phenotype), we tested whether an additional male might make the respective male phenotypes more interesting to females, by including sexual motivation but excluding the information that can be gained by observing a pair.

## METHODS

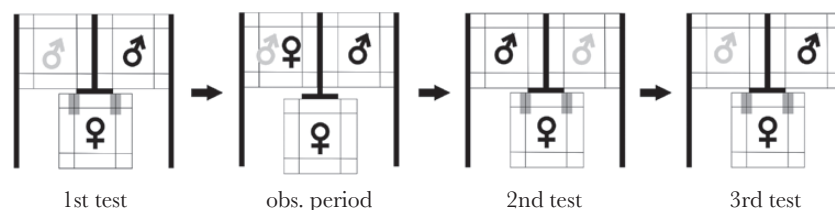
### Study species

Test birds were sexually mature descendants of wild zebra finches that were exported from Northern Victoria, Australia, in 1992 (Meyer T, personal communication). They were kept in up to 6 aviaries ( $2 \times 1.65 \times 2.30 \text{ m}^3$  and  $2.25 \times 1.05 \times 2.30 \text{ m}^3$ ), separated by sex after maturation (mean 71, minimum 56, and maximum 92 days after hatching) for at least 6 months before the experiments. The air-conditioned room ( $6.80 \times 4 \times 2.40 \text{ m}^3$ ) ( $T = 24 \pm 1 \text{ }^\circ\text{C}$ ,  $H = 60 \pm \text{max. } 10\%$ ) with windows at 2 sides was illuminated with fluorescent lighting including UV range at a 14:10 h light:dark photoperiod. Both sexes wore numbered orange leg bands, white leg bands, or silver metal leg bands (neutral in zebra finch mate choice). Each aviary contained several branches, coconut fibers for nest building, several nest-boxes, and sand and food ad libitum. Zebra finches were fed daily with a mixture of seeds containing Senegal, red, yellow, and Canary millets; sprouted birdseed; and cucumber, chickweed, and crunched eggshells.

### Experiments

All experiments and controls were conducted in a room ( $2.20 \times 2.10 \times 2.40 \text{ m}^3$ ) under the same conditions as in the aviary room. Experiments and controls were performed in cages (each  $49 \times 43 \times 50 \text{ cm}^3$ ); stimulus birds were placed side by side, and the test bird was placed centrally in front of them (Figure 1). Each cage contained water, food, and sand ad libitum in little bowls on the ground and 4 perches: 1 low perch parallel and near to the front (10 cm above the bottom of the cage), 1 high perch parallel and near to the backside (35 cm), and 2 additional perches parallel and near to the side of the cage in middle height (20 cm). Several wooden screens, placed between the stimulus cages and around the whole setup, prevented visual contact between the stimulus birds before starting the experiments and between the phases of an experiment. An additional paper screen (18 cm wide and 49 cm high), fixed vertically to the front and in the middle of the test birds cage, prevented the test bird from seeing both stimulus birds at the same time when being in direct proximity of one of the stimulus cages.

All birds were kept in test cages at least 15 h before we started the experiments the next morning in visual but not acoustic



**Figure 1**

Experimental setup for female mate-choice tests, top-view. 1st test = first mate-choice test, obs. period = observation period, 2nd test = second mate-choice test, 3rd test = third mate-choice test. Gray male symbols = adorned, black male and female symbols = unadorned. Gray areas are mate-choice zones. Thin lines are perches, and bold lines are screens. The position of stimulus cages was switched within a mate-choice test. We used new stimulus males for each test phase.

isolation from other birds. Stimulus birds were adorned with either a red feather or a piece of a gray flight feather (unadorned) before placing them into their cages 1 day before testing (for pictures of the adornment, [Supplementary Figure S1](#)). Red feathers were cut out of a red feather boa along the quill (length: 2 cm, width: 4–5 mm). Gray flight feathers were cut to triangles (maximum edge length 5 mm). Both were glued to the forehead with double-sided tape onto their natural forehead feathers, which could easily be removed afterward. This way, all stimulus birds were handled equally.

### General procedure

In the first mate-choice test, test birds could choose between an adorned (red feather) and an unadorned opposite sex stimulus bird to determine the initial mate preference and to test whether test birds had a latent, that is, genetically determined, preference for the novel phenotype in the opposite sex ([Table 1](#)). During the observation period, test birds could observe new stimulus birds, 1 single unadorned bird in 1 cage and 1 adorned bird with its unadorned mate in the other cage. The respective pairs were taken from their breeding cage and transferred to the stimulus cage. They had been together for several months and had reproduced with each other. After this observation period, test birds again got the opportunity to choose between 2 new stimulus birds, 1 adorned and 1 unadorned (second mate-choice test). The third mate-choice test was identical to the second mate-choice test, but with new stimulus birds. Between the different phases, we gave birds the time to acclimate for at least 5 min and up to 10 min when necessary. We exchanged stimulus birds between each phase because we wanted to test whether males and females generalize and prefer the phenotype observed instead of the same individual.

### Mate-choice copying experiments in females

By removing the screens, we started the first mate-choice test, which lasted  $2 \times 20$  min with a switch of stimulus male cages after 20 min to control for side biases. We measured the time (s) the test female spent perching on the outer one-third of the perches of choice adjacent to the stimulus males (mate-choice zone; gray area in [Figure 1](#)) every 10 s. If the test female changed position during the 10-s interval, 5 s were scored, otherwise 10 s. All other positions, which included the greater part of the cage (e.g. feeding on the ground or sitting on the other perches), were scored as no choice positions. Thus, the choice positions covered only 16% of all possible perching positions. This method is an established measurement to determine sexual preferences in zebra finches ([Witte 2006b](#)). We calculated their choosing motivation (total time spent in both mate-choice zones during the  $2 \times 20$  min mate-choice test). Additionally, we counted the number of courtship displays (whether or not males

sang within a 10-s interval, either directed or undirected). Male song rate is known to influence female mate choice as they spend more time with males that sing more often compared with those that sing less often ([Forstmeier and Birkhead 2004](#)). Additionally, we were able to compare male singing activity as it is known that social feedback is important in mate choice ([Collins 1994](#); [Royle and Pike 2010](#)). During the observation period, which lasted 2 h, the female observed a new, single, unadorned male in 1 cage and a new, adorned male together with his unadorned female partner in another stimulus cage ([Table 1](#)). The side where the pair was presented was randomized. The second and third mate-choice tests were performed like the first mate-choice test, but with new stimulus males. After each experiment, we measured the body weight of all birds and placed them back into their aviaries or cages. We used each test female only once. Stimulus males were used for up to 3 mate-choice tests, but always in different combinations and both as an adorned or an unadorned stimulus.

Throughout the whole testing time (10 min before starting the first mate-choice test until the last mate-choice test was over), we played zebra finch sounds (recorded in the aviary room) through a loudspeaker (Speed Link, Brave 2.0 Stereo Sound System). Because zebra finches live in flocks, they tend to be relatively inactive if they do not hear calls of conspecifics. We placed the loudspeakers on the ground, about 30 cm away from the table on which we placed the test female. The sound was played at about 60–70 db, measurements depending on the type of sounds the birds made. This equals the sound pressure level measured in the middle of our aviary room.

Test birds that showed side biases during the first mate-choice test, those that spent more than 80% of their choosing time on the same side, even though we switched the position of the stimulus cages, were excluded from the analysis in accordance with other studies ([Schlupp and Ryan 1997](#); [Dosen and Montgomerie 2004](#); [Hoysak and Godin 2007](#); [Williams and Mendelson 2010](#)). We tested a total number of 26 females in the female mate-choice copying experiments.

### Mate-choice copying experiments in males

Mate-choice copying experiments in males were performed with the same design and after the same protocol as the mate-choice copying experiments in females. Stimulus females were either unadorned or adorned with the red feather on the forehead. The stimulus pair in the observation period consisted of an adorned female with her unadorned male partner ([Table 1](#)). We tested a total number of 26 males in male mate-choice copying experiments.

### Controls

We performed several controls to test alternative explanations for a potential change in mate-choice decisions in females.

**Table 1**  
Overview of the phases in experiments and controls

Experiments/controls	N	Test period (month)	First test	Obs. period	Second test	Third test
Female experiments	24	IV–X 2009	♂/♂	♂/♂ ♀	♂/♂	♂/♂
Female control for consistency	18	X–XII 2010	♂/♂	♂/♂	♂/♂	♂/♂
Female control for social/local enhancement	15	VIII–XI 2011	♀/♀	♀/♀ ♀	♀/♀	—
Female control for sociosexual/local enhancement A	15	VIII–XI 2011	♂/♂	♂/♂♂	♂/♂	—
Female control for sociosexual/local enhancement B	15	VIII–XI 2011	♂/♂	♂/♂♂	♂/♂	—
Male experiments	20	IV–X 2009	♀/♀	♀/♀♂	♀/♀	♀/♀

First test = first mate-choice test, obs. period = observation period, second test = second mate-choice test, and third test = third mate-choice test. Gray male/female symbols = adorned birds and black male/female symbols = unadorned birds.

### **Control for consistency in female mate choice when no public information is provided**

In this control, we tested whether females would choose consistently between males of 2 different phenotypes when no public information was provided. Controls were conducted after the same protocol as described above but with a few changes in the design. Cages of the test females were larger ( $97 \times 43 \times 52 \text{ cm}^3$ ) due to technical reasons (comparability to other mate-choice copying experiments in our lab, unpublished data) and had 2 additional perches of choice in middle height. During the observation period, we presented 2 single males (1 adorned and 1 unadorned). Therefore, we provided no public information about the quality of potential mates (Table 1). We tested a total number of 19 females.

### **Control for social and local enhancement in female mate choice**

Due to the fact that a pair of birds, a male and a female, was presented during the observation period in the mate-choice copying experiments, we tested whether the presentation of 2 females (1 adorned and 1 unadorned) versus 1 unadorned female bird (social enhancement) can explain a possible change in mate choice in females (Table 1). If social enhancement is the reason for a change in mate choice in females, females should prefer the female phenotype they have seen together with another female during the observation period.

Experiments were conducted after the same protocol as described above, but we left out the third mate-choice test. We tested a total number of 17 females.

### **Control for sociosexual and local enhancement in female mate choice**

This control was performed after the same protocol as the control for social and local enhancement, but we used male stimulus birds only. During the observation period, we presented females with a single male in 1 cage and 2 males in the other cage (Table 1). Because we had 2 different male phenotypes, we performed this control in 2 different versions (A and B).

#### **Version A**

Presentation of a single unadorned male in 1 cage and an adorned and an unadorned male in the other cage (Table 1). We tested a total number of 16 females.

#### **Version B**

Presentation of a single adorned male in 1 cage and 2 unadorned males in the other cage (Table 1). We tested a total number of 15 females.

Hence, we presented a stimulus that was a combination of social (2 same-sex birds that were not a pair) and sexual (males as potential partners), but without the information a heterosexual pair would provide inadvertently.

### **Statistical analysis**

We analyzed the time test birds spent within the mate-choice zones in front of stimulus birds. We used mate-choice scores of time spent with the adorned stimulus (time spent with the adorned stimulus/time spent with both the adorned and the unadorned stimuli) and tested whether this was influenced by test number. We transformed mate-choice scores via arcsine square root to have normally distributed data and used a repeated-measures Anova (rmAnova) (with mate-choice test as within-subject factor). Where Anova results did

not conform to the assumption of sphericity, Greenhouse–Geisser approximations were used. To test whether test birds showed a preference for 1 of the 2 stimulus birds, we tested the mate-choice scores of time spent with adorned males against a 50% expectation using a 1-sample *t*-test.

To compare number of intervals with song of stimulus males, we used a Kruskal–Wallis test; to compare weight of stimulus birds, we used an unpaired *t*-test; to compare number of intervals with song of test males and to analyze choosing motivation, we used a Friedman test as well as a Wilcoxon test.

To test whether time spent with adorned males during the first mate-choice test differed across the 4 experiments in which females could choose between an adorned and unadorned male, we compared mate-choice scores using a univariate Anova and a post hoc test with Bonferroni correction to allow pairwise comparisons.

Statistical analyses were performed using SPSS (IBM SPSS Statistics 22). All *P* values are 2-tailed.

## **RESULTS**

### **Mate-choice copying experiments in females**

We excluded 1 female because of a side bias and 1 additional female because she refused to move at all during the first mate-choice test, leaving 24 females. There was no change in choosing motivation (i.e., sum of time spent with both males) throughout the whole mate-choice copying test, including 3 mate-choice tests (Friedman test:  $\chi^2 = 1.583$ , degrees of freedom [df] = 2,  $P = 0.453$ ,  $n = 24$ ). Mate-choice scores of time spent with adorned males were affected by test number (rmAnova:  $F_{1,3,30,2} = 13.483$ ,  $P < 0.001$ ; Figure 2a and Supplementary Material). Mate-choice score of time spent with adorned males increased between the first and the second and the first and the third mate-choice test. Females showed no preference for adorned or unadorned males during the first mate-choice test (1-sample *t*-test:  $t = -0.343$ ,  $df = 23$ ,  $P = 0.735$ ), but after obtaining public information, they preferred adorned males over unadorned males in the second mate-choice test (1-sample *t*-test:  $t = 5.743$ ,  $df = 23$ ,  $P < 0.001$ ) and the third mate-choice test (1-sample *t*-test:  $t = 6.320$ ,  $df = 23$ ,  $P < 0.001$ ). Adorned and unadorned males did not differ in number of intervals with song or in their weight (Supplementary Material).

### **Mate-choice copying experiments in males**

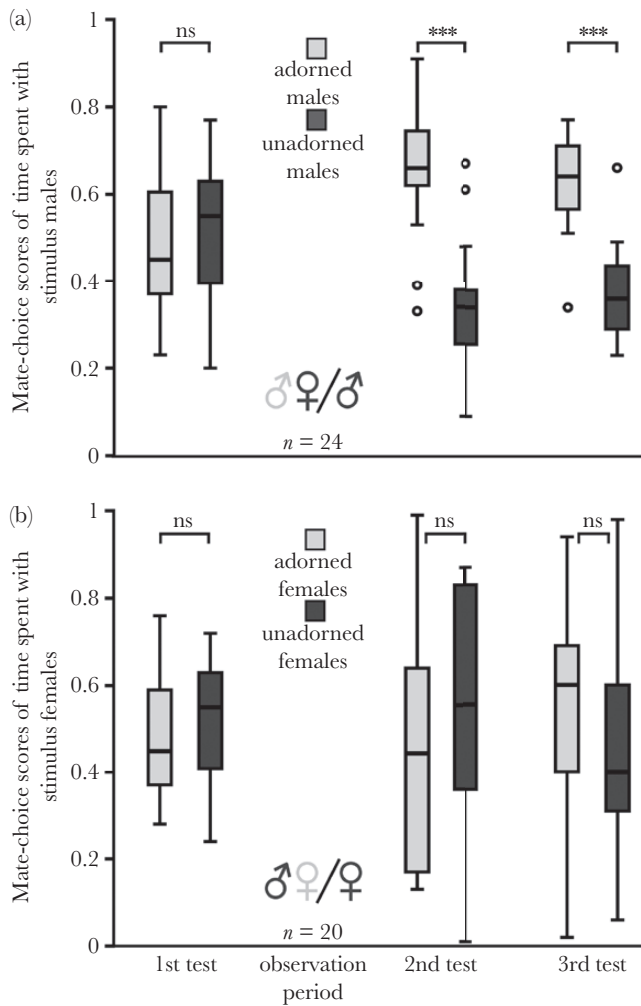
We excluded 6 males because of side biases, leaving 20 males. Choosing motivation changed between the 3 mate-choice tests (Friedman test:  $\chi^2 = 7.900$ ,  $df = 2$ ,  $P = 0.019$ ,  $n = 20$ ). Males spent more time choosing in the second than in the first mate-choice test (paired *t*-test:  $t = -4.056$ ,  $df = 19$ ,  $P = 0.001$ ). In contrast to females, male mate-choice scores of time spent with adorned females were not affected by test number (rmAnova:  $F_{2,38} = 1.396$ ,  $P = 0.260$ ; Figure 2b and Supplementary Material). Males showed no preference for adorned or unadorned females during the 3 mate-choice tests (1-sample *t*-test: all  $P > 0.394$ ). Adorned and unadorned females did not differ in weight, and test males did not sing more to either of the female types (Supplementary Material).

### **Controls**

#### **Control for consistency in female mate choice when no public information is provided**

We excluded 1 female because of a side bias, leaving 18 females. There was no change in choosing motivation throughout the 3



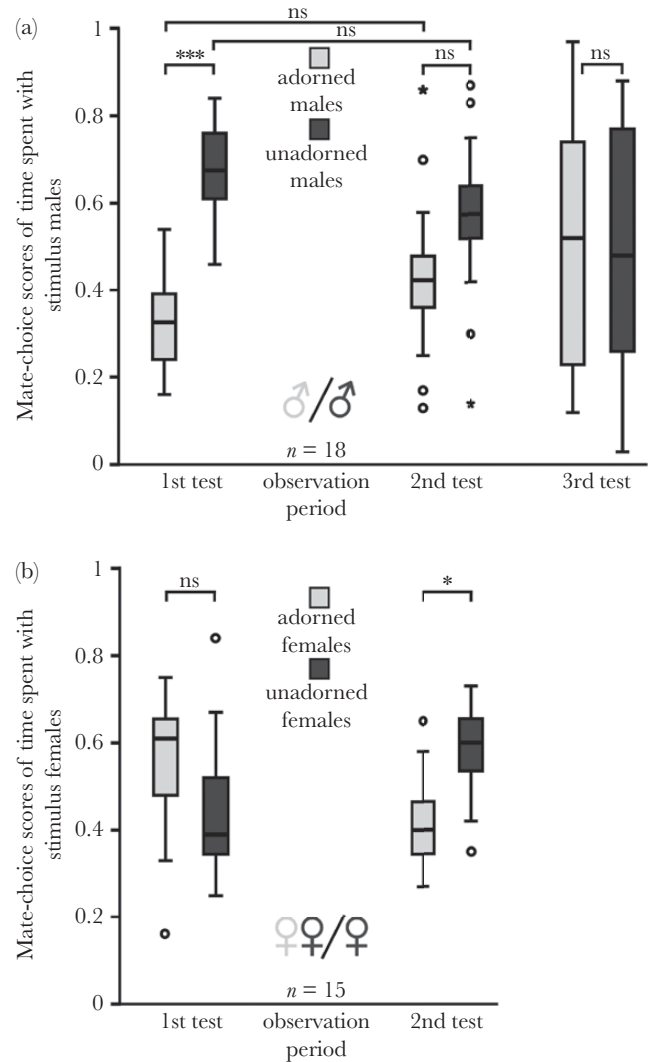


**Figure 2** Mate-choice copying experiments in females (a) and males (b). Box plot showing median, first and third quartile, 95% confidence limits and open points as outliers for mate-choice scores of time spent with stimulus birds. 1st test = first mate-choice test, 2nd test = second mate-choice test, 3rd test = third mate-choice test. Gray male/female symbols = adorned and black male/female symbols = unadorned. \*\*\* $P < 0.001$  and ns = nonsignificant.

mate-choice tests (Friedman test:  $\chi^2 = 0$ ,  $df = 2$ ,  $P = 1$ ,  $n = 18$ ). Mate-choice scores of time spent with adorned males were affected by test number (rmAnova:  $F_{1,4,24.4} = 3.849$ ,  $P = 0.048$ ; Figure 3a and Supplementary Material). However, changes in mate-choice scores of time spent with the adorned male between the mate-choice tests were not significant (paired  $t$ -tests: all  $P > 0.168$ ). Females preferred unadorned over adorned males during the first mate-choice test (1-sample  $t$ -test:  $t = -7.132$ ,  $df = 17$ ,  $P < 0.001$ ), but they did not prefer one of the males during the second and the third mate-choice tests (1-sample  $t$ -test: both  $P > 0.120$ ). Adorned and unadorned males did not differ in number of intervals with song or in their weight (Supplementary Material).

**Control for social and local enhancement in female mate choice**

We excluded 2 females because of side biases, leaving 15 females. There was no change in choosing motivation (Wilcoxon test:  $Z = -0.625$ ,  $P = 0.532$ ,  $n = 15$ ). Mate-choice scores of time spent



**Figure 3** Control for (a) consistency in female mate choice when no public information is provided and (b) social and local enhancement in female mate choice. Box plot showing median, first and third quartile, 95% confidence limits and open points as outliers and stars as extremes for mate-choice scores of time spent with stimulus males. 1st test = first mate-choice test, 2nd test = second mate-choice test, and 3rd test = third mate-choice test. Gray male/female symbols = adorned and black male/female symbols = unadorned. \* $P < 0.05$ , \*\*\* $P < 0.001$ , ns = nonsignificant.

with adorned females were affected by test number (rmAnova:  $F_{1,14} = 6.581$ ,  $P = 0.022$ ; Figure 3b and Supplementary Material). Females showed no preference for adorned or unadorned females during the first mate-choice test (1-sample  $t$ -test:  $t = 1.120$ ,  $df = 14$ ,  $P = 0.282$ ), but they preferred unadorned females over adorned females in the second mate-choice test (1-sample  $t$ -test:  $t = -3.140$ ,  $df = 14$ ,  $P = 0.007$ ). Adorned and unadorned females did not differ in weight (Supplementary Material).

**Control for sociosexual and local enhancement in female mate choice**

**Version A**

We excluded 1 female because of a side bias, leaving 15 females. There was no decline in choosing motivation (Wilcoxon test:

$\zeta = -0.511$ ,  $P = 0.609$ ,  $n = 15$ ). Mate-choice scores of time spent with adorned males were affected by test number (rmAnova:  $F_{1,14} = 6.016$ ,  $P = 0.028$ ; [Supplementary Material](#)). Females spent less time with adorned males in the second mate-choice test than in the first mate-choice test. Females did not show a preference for adorned or unadorned males during both mate-choice tests (1-sample  $t$ -test: both  $P = 0.094$ ). Adorned and unadorned males did not differ in number of intervals with song or in their weight ([Supplementary Material](#)).

### Version B

There was no change in choosing motivation (Wilcoxon test:  $\zeta = -1.108$ ,  $P = 0.268$ ,  $n = 15$ ). Mate-choice scores of time spent with adorned males were not affected by test number (rmAnova:  $F_{1,14} = 0.011$ ,  $P = 0.917$ ; [Supplementary Material](#)). Females did not show a preference for adorned or unadorned males during both mate-choice tests (1-sample  $t$ -test: both  $P = 0.815$ ). Adorned and unadorned males did not differ in number of intervals with song, but they differed in weight ([Supplementary Material](#)).

### Comparison of the first mate-choice tests between female experiment and controls

Female mate-choice scores of time spent with adorned males during the first mate-choice tests were different across the 4 experiments in which females could choose between an adorned and an unadorned male (Anova:  $F_{3,68} = 6.710$ ,  $P < 0.001$ ).

## DISCUSSION

We found that female zebra finches changed their mate preference for males adorned with a red feather after observing a single unadorned male and a pair where the male was adorned. They preferred adorned males and thus showed a preference for the novel phenotype. Males, on the other hand, did not change their mate preference after observing a single female and a pair where the female was adorned. Results of controls could not provide alternative explanations for the increase in time that females spent with the novel phenotype. Therefore, females copied the mate choice of other females for a novel phenotype, whereas males did not.

We used the novel trait as an indicator to test if and how strong nongenetic factors can lead to the development of a new preference and potentially contribute to the spread of a novel trait within a population in zebra finches. During the first mate-choice tests, neither females nor males showed a preference for the novel phenotype. Thus, neither sex had a latent intrinsic preference for this new phenotypic trait in the opposite sex. Our results are consistent with other experiments in this species, showing that neither sex had a latent preference for an artificial red feather (Witte and Sawka 2003) or an artificial blue feather (Witte and Caspers 2006). However, Burley and Symanski (1998) found that zebra finch females had a latent preference for conspecifics of the opposite sex with a white crest feather, whereas male zebra finches preferred females without crest feathers.

In our experiment, females used the presented public information to assess the suitability, that is, quality, of the adorned males and integrated this into their own mate-choice decisions. This is consistent with results of Swaddle et al. (2005), who showed that female zebra finches preferred individual males and also males of the same phenotype (same leg band color) that were apparently chosen by other females, after 2 weeks of observation. Our experiments now show that an observation period of a single pair of only

2 h is sufficient for females to copy the mate choice for a male phenotype. Our results are also consistent with experiments by Drullion and Dubois (2008), who found that female zebra finches copied the mate choice of their conspecifics when the provided information was consistent. It is known that male song can influence female mate choice (reviewed in Clayton 1990; Riebel 2009), which is why we counted the number of male song bouts as females may have spent more time with males that sang more often (Forstmeier and Birkhead 2004). Number of song bouts did not differ between the respective stimulus males, suggesting that the visual cue of wearing the red feather altered females' mate choices. The effect of the observation of public information, therefore, seems to have been relatively strong.

What are the advantages of mate-choice copying for zebra finch females? Females that copy the mate choice of other females may be able to reduce potential costs, such as a high predation risk or time and energy to assess a male's suitability, that is, quality, as a mate (Pomiankowski 1987; Gibson and Höglund 1992; Pruett-Jones 1992; Dugatkin and Höglund 1995). Because the zebra finch is an opportunistic breeder, females are bound to find a mate quickly when conditions are good for breeding. These may be either young females when they reach the age to start breeding or older females when they have lost their mate due to mortality (Zann 1996) or divorce (Morris 1954). This time constraint (Jennions and Petrie 1997) may limit their opportunity to adequately search for the best possible mate by sampling among males. And because the zebra finch is a socially monogamous species, access to males is limited. Choosing the wrong male can bear large costs for females. Using public information can help females to find a good mate, a male of the same phenotype that another female has chosen, in a relatively short time period, therefore enabling them to breed under good conditions. Living in flocks provides them with opportunities to gain the information they need. However, this information can be inconsistent and females will encounter contradicting public information during their mate choice in the wild. The results of Drullion and Dubois (2008) suggest that females will rely on their own information if they gain inconsistent public information. Dubois et al. (2012) have shown in their theoretical model that the use of private and social information can coexist in a population. Whether there may be fitness benefits for copier females, or for the copied males, remains to be tested. Regarding the facts that access to males is limited and that females need to receive consistent public information (Drullion and Dubois 2008), copying in the wild will most likely be bound to specific circumstances in order to occur. The preference for a new trait will be copied either if the trait has already spread throughout the population and females may see a number of other females paired to males of such a phenotype or if there are only a few pairs around and by chance the new trait was chosen. A theoretical study by Agrawal (2001) considers mate-choice copying an efficient mechanism for the evolution of new traits (but see Kirkpatrick and Dugatkin 1994). Agrawal showed that mate-choice copying can support the spread of a novel trait within a population and that it can drive females to prefer rare and novel male phenotypes. And an experimental study on sailfin mollies (*Poecilia latipinna*) showed that female mate-choice copying can support the spread of a new male trait in this species (Witte 2006a). The new trait will not replace the current natural phenotype as there will always be a majority of females paired to such males. However, in the above-mentioned circumstances, females will socially learn mate preferences for males with new sexual traits, which would aid the spread of the new phenotype. Mate-choice copying may work in the same way for natural male traits and thus might lead to an increase

in phenotype variation in males. This is a novel aspect of mate-choice copying. Sexual selection in general may lead to a decrease in male variation due to the fact that it usually drives females to choose an optimum. Mate-choice copying, however, might be one mechanism that can sustain variation between males or even increase this variation regarding male traits.

Males did not copy the mate choice of other males. They spent a similar amount of time with both females during the first mate-choice test. They did the same during the second and third mate-choice tests after they had observed a single, unadorned female and another adorned female with her male mate. In general, mate-choice copying may enhance sperm competition in males. However, when males copy the choice for a female phenotype, there is less sperm competition compared to when they copy the choice for an individual female. To assess females, they seem to rely on information other than the female phenotype and the mate choice of other males in the situation we presented. For example, males may choose females that are more fecund, that is, produce more eggs (Monaghan et al. 1996; Jones et al. 2001), but in those studies, no relationship was found between fecundity and female body size or mass, indicating that there is no obvious connection between a females' quality and her phenotype. More subtle cues may be used by males to determine fecundity and therefore quality.

Although it is known that artificial ornaments and specific colors can have an influence on male mate-choice decisions in zebra finches (e.g. Burley et al. 1982), the red feather did not make females more or less attractive to males in our experiment. Because the color red seems to be a more male-specific trait in the zebra finch (Burley and Coopersmith 1987), males might recognize females with a red feather on the head as male-like females and therefore as a negative stimulus (Weary et al. 1993). Another point is that experiments of Burley and Symanski (1998) have shown that males prefer uncrested females over those wearing a white crest feather. Both factors could have made males reluctant to copy. Although males have been found to learn a preference for white crested females via sexual imprinting (Burley 2006) and are thereby capable of learning a preference for an artificial trait, they did not imprint on blue (Witte and Caspers 2006) or red (Witte and Sawka 2003) crest feathers, in contrast to females. Finally, males may simply not be able to generalize an observed preference for a new trait to the same extent as females.

Our results that females copied the mate choice, but males did not, are consistent with the results of Côté et al. (Côté K, Dubois F, Giraldeau L-A, Witte K, unpublished data) where male zebra finches also did not copy the mate-choice decisions of conspecific males. To our knowledge, there is no published data on mate-choice copying in male zebra finches so far. Sex differences in mate-choice copying have been shown for other species, too. For example, in pipefish, a sex-role reversed species, males but not females copy the mate choice of their conspecifics (Widemo 2005). Additionally, Moran et al. (2013) found that male but not female darters of *Etheostoma flabellare* copy the mate choice of their conspecifics.

Our results not only show that female zebra finches copy other females' mate choice, that is, use public information, whereas males do not, but they also show that females generalize and copy the choice for a phenotype, which is consistent with the results of Swaddle et al. (2005). Generalization is a fundamental prerequisite for the cultural inheritance of mate preferences (Brooks 1998; Plenge et al. 2000; Witte and Noltemeier 2002; Godin et al. 2005). Because we used new males for each mate-choice test (generalization of a preference for a phenotype) and we could show that females maintained this copied preference for longer than one

mating event (third mate-choice test), we found evidence for cultural inheritance of mate preferences (Boyd and Richerson 1985; Brooks 1998; Godin et al. 2005) in this species.

In all but one first mate-choice tests, females did not discriminate between the unadorned and adorned males. In the control for mate-choice consistency, however, where females had no opportunity to copy, females preferred the unadorned phenotype, but lost this preference after the observation period. Further analysis revealed that females spent a similar amount of time with adorned males across the experiments and controls. The preference for unadorned males in the control for consistency was due to a higher amount of time spent with unadorned males, which reduced the time spent outside the mate-choice area, but not the time spent with adorned males. Red is already known to be a favored color in female zebra finch mate choice, and the loss of preference might arise because of females becoming more familiar with the new phenotype over time. But we cannot find a change consistent with this in our other controls. Additionally, experiments by Drullion and Dubois (2008) demonstrate that females show mate-choice copying when other colors instead of red are used (white and orange). In our control for consistency, there was no change in mate-choice scores of time spent with either male phenotype between the 3 mate-choice tests as there was in the experiment. Thus, females chose consistently in the control when no public information was provided compared to the mate-choice copying experiments. Our other controls showed that neither social nor sociosexual or local enhancement can be responsible for the change in mate choice in female zebra finches. Contrary to our experiment, females either showed no preference for the stimulus males or preferred the unadorned stimulus females.

Our experiments showed that female zebra finches copy and generalize the mate choice for an artificial new secondary sexual male trait (a red feather on the forehead), whereas male zebra finches do not. The fact that female zebra finches use public information in the context of mate choice amplifies the dynamic in the evolutionary processes of sexual selection. It demonstrates that mate-choice copying can be a mechanism for the distribution of new mate preferences and new secondary traits in a biparental, socially monogamous species under certain circumstances and that it fulfills the requirement of cultural transmission.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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## REFERENCES

- Agrawal AF. 2001. The evolutionary consequences of mate copying on male traits. *Behav Ecol Sociobiol.* 51:33–40.
- Arnqvist G. 2006. Sensory exploitation and sexual conflict. *Phil Trans R Soc B.* 361:375–386.
- Auld HL, Punzalan D, Godin J-GJ, Rundle HD. 2009. Do female fruit flies (*Drosophila serrata*) copy the mate choice of others? *Behav Process.* 82:78–80.
- Bakker TCM, Pomiankowski A. 1995. The genetic basis of female mate preferences. *J Evol Biol.* 8:129–171.
- Bowers RI, Place SS, Todd PM, Penke L, Asendorpf JB. 2012. Generalization in mate-choice copying in humans. *Behav Ecol.* 23:112–124.
- Boyd R, Richerson PJ. 1985. *Culture and the evolutionary process.* Chicago (IL): University of Chicago Press.
- Brooks R. 1998. The importance of mate copying and cultural inheritance of mating preferences. *Trends Ecol Evol.* 13:45–46.
- Burley NT. 2006. An eye for detail: selective sexual imprinting in zebra finches. *Evolution.* 148:145–155.
- Burley N, Coopersmith C. 1987. Bill color preferences of zebra finches. *Ethology.* 76:133–151.
- Burley N, Krantzberg G, Radman P. 1982. Influence of colour-banding on the conspecific preferences of zebra finches. *Anim Behav.* 30:444–455.
- Burley NT, Symanski R. 1998. “A taste for the beautiful”: latent aesthetic mate preferences for white crests in two species of Australian grass-finches. *Am Nat.* 152:792–802.
- Clayton NS. 1990. Assortative mating in zebra finch subspecies, *Taeniopygia guttata guttata* and *T. g. castanotis*. *Phil Trans R Soc B Biol Sci.* 330:351–370.
- Collins SA. 1994. Male displays: cause or effect of female preference? *Anim Behav.* 48:371–375.
- Dall SR, Giraldeau LA, Olsson O, McNamara JM, Stephens DW. 2005. Information and its use by animals in evolutionary ecology. *Trends Ecol Evol.* 20:187–193.
- Danchin E, Giraldeau LA, Valone TJ, Wagner RH. 2004. Public information: from nosy neighbors to cultural evolution. *Science.* 305:487–491.
- DeKogel K, Prijs HJ. 1996. Effects of brood size manipulations on sexual attractiveness of offspring in the zebra finch. *Anim Behav.* 51:699–708.
- van Doorn GS, Edelaar P, Weissing FJ. 2009. On the origin of species by natural and sexual selection. *Science.* 326:1704–1707.
- Dosen LD, Montgomerie R. 2004. Female size influences mate preferences of male guppies. *Ethology.* 110:245–255.
- Doucet M, Yezerinac SM, Montgomerie R. 2004. Do female zebra finches (*Taeniopygia guttata*) copy each other's mate preferences? *Can J Zool.* 82:1–7.
- Drullion D, Dubois F. 2008. Mate-choice copying by female zebra finches, *Taeniopygia guttata*: what happens when model females provide inconsistent information? *Behav Ecol Sociobiol.* 63:269–276.
- Dubois F, Drullion D, Witte K. 2012. Social information use may lead to maladaptive decisions: a game theoretic model. *Behav Ecol.* 23:225–231.
- Dugatkin LA. 1996. Interface between culturally based preferences and genetic preferences: female mate choice in *Poecilia reticulata*. *Proc Natl Acad Sci USA.* 93:2770–2773.
- Dugatkin LA. 1998. Genes, copying, and female mate choice: shifting thresholds. *Behav Ecol.* 9:323–327.
- Dugatkin LA, Höglund J. 1995. Delayed breeding and the evolution of mate copying in lekking species. *J Theor Biol.* 174:261–267.
- Fisher RA. 1930. *The genetical theory of natural selection.* Oxford: Clarendon Press.
- Forstmeier W, Birkhead TR. 2004. Repeatability of mate choice in the zebra finch: consistency within and between females. *Anim Behav.* 68:1017–1028.
- Galef BG Jr, Lim TCW, Gilbert GS. 2008. Evidence of mate choice copying in Norway rats, *Rattus norvegicus*. *Anim Behav.* 75:1117–1123.
- Gibson RM, Bradbury JW, Vehrencamp SL. 1991. Mate choice in lekking sage grouse revisited: the roles of vocal display, female site fidelity, and copying. *Behav Ecol.* 2:165–180.
- Gibson RM, Höglund J. 1992. Copying and sexual selection. *Trends Ecol Evol.* 7:229–232.
- Godin J-GJ, Herdmann EJE, Dugatkin LA. 2005. Social influences on female mate choice in the guppy, *Poecilia reticulata*: generalized and repeatable trait-copying behaviour. *Anim Behav.* 69:999–1005.
- Goodwin D. 1982. *Estrildid finches of the World.* Oxford: British Museum (Natural History), Oxford Univ. Press.
- Heyes CM, Ray ED, Mitchell CJ, Nokes T. 2000. Stimulus enhancement: control for social facilitation and local enhancement. *Learn Motiv.* 31:83–98.
- Höglund J, Alatalo RV, Gibson RM, Lundberg A. 1995. Mate-choice copying in black grouse. *Anim Behav.* 49:1627–1633.
- Hoysak DJ, Godin J-GJ. 2007. Repeatability of male mate choice in the mosquitofish, *Gambusia holbrooki*. *Ethology.* 113:1007–1018.
- Iwasa Y, Pomiankowski A. 1999. Good parent and good genes models of handicap evolution. *J Theor Biol.* 200:97–109.
- Jennions MD, Petrie M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev.* 72:283–327.
- Jones KM, Monaghan P, Nager RG. 2001. Male mate choice and female fecundity in zebra finches. *Anim Behav.* 62:1021–1026.
- Kirkpatrick M, Dugatkin LA. 1994. Sexual selection and the evolutionary effects of copying mate choice. *Behav Ecol Sociobiol.* 34:443–449.
- Kokko H, Brooks R, Jennions MD, Morley J. 2003. The evolution of mate choice and mating biases. *Proc R Soc B.* 270:653–664.
- Loyau A, Blanchet S, Van Laere P, Clobert J, Danchin E. 2012. When not to copy: female fruit flies use sophisticated public information to avoid mated males. *Sci Rep.* 2:768.
- Maan ME, Seehausen O. 2011. Ecology, sexual selection and speciation. *Ecol Lett.* 14:591–602.
- Mead LS, Arnold SJ. 2004. Quantitative genetic models of sexual selection. *Trends Ecol Evol.* 19:264–271.
- Mery F, Varela SA, Danchin E, Blanchet S, Parejo D, Coolen I, Wagner RH. 2009. Public versus personal information for mate copying in an invertebrate. *Curr Biol.* 19:730–734.
- Monaghan P, Metcalfe NB, Houston DC. 1996. Male finches selectively pair with fecund females. *Proc R Soc B.* 263:1183–1186.
- Moran RL, von Ende CN, King BH. 2013. Mate choice copying in two species of darters (Percidae: Etheostoma). *Behaviour.* 150:1255–1274.
- Morris D. 1954. The reproductive behavior of the Zebra Finch (*Poephila guttata*) with special reference to pseudofemale behavior and displacement activities. *Behaviour.* 7:1–31.
- Nöbel S, Witte K. 2011. Learning and mate choice. In: Brown C, Laland K, Krause J, editors. *Fish cognition and behavior.* 2nd ed. Oxford: Blackwell Publishing p. 85–107.
- Pfennig DW, Wund MA, Snell-Rood EC, Cruickshank T, Schlichting CD, Moczek AP. 2010. Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol Evol.* 25:459–467.
- Plenge M, Curio E, Witte K. 2000. Sexual imprinting supports the evolution of a novel trait by transference of a preference for the colour red. *Behaviour.* 137:741–758.
- Pomiankowski A. 1987. The costs of choice in sexual selection. *J Theor Biol.* 128:195–218.
- Pruett-Jones S. 1992. Independent versus nonindependent mate choice: do females copy each other? *Am Nat.* 140:1000–1009.
- Riebel K. 2009. Song and female mate choice in zebra finches: a review. *Adv Stud Behav.* 40:197–238.
- Royle NJ, Pike TW. 2010. Social feedback and attractiveness in zebra finches. *Behav Ecol Sociobiol.* 64:2015–2020.
- Ruell EW, Handelsman CA, Hawkins CL, Sofaer HR, Ghalambor CK, Angeloni L. 2013. Fear, food and sexual ornamentation: plasticity of colour development in Trinidadian guppies. *Proc R Soc B.* 280:2012–2019.
- Schlupp I, Ryan MJ. 1997. Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males. *Behav Ecol.* 8:104–107.
- Simons MJP, Verhulst S. 2011. Zebra finch females prefer males with redder bills independent of song rate—a meta-analysis. *Behav Ecol.* 22:755–762.
- Swaddle JP, Cathey MG, Correll M, Hodkinson BP. 2005. Socially transmitted mate preferences in a monogamous bird: a non-genetic mechanism of sexual selection. *Proc R Soc B.* 272:1053–1058.
- Swaddle JP, Cuthill IC. 1994. Female zebra finches prefer males with symmetric chest plumage. *Proc R Soc B.* 258:267–271.
- Weary DM, Guilford TC, Weisman RG. 1993. A product of discriminative learning may lead to female preferences for elaborate males. *Evolution.* 47:333–336.
- Westneat DF, Walters A, McCarthy TM, Hatch MI, Hein WK. 2000. Alternative mechanisms of nonindependent mate choice. *Anim Behav.* 59:467–476.
- White DJ, Galef BG Jr. 2000. ‘Culture’ in quail: social influences on mate choices of female *Coturnix japonica*. *Anim Behav.* 59:975–979.
- Widemo MS. 2005. Male but not female pipefish copy mate choice. *Behav Ecol.* 17:255–259.



- Williams TH, Mendelson TC. 2010. Behavioral isolation based on visual signals in a sympatric pair of darter species. *Ethology*. 116:1038–1049.
- Witte K. 2006a. Learning and mate choice. In: Brown C, Laland K, Krause J, editors. *Fish cognition and behavior*. Oxford: Blackwell Publishing. p. 70–95.
- Witte K. 2006b. Time spent is a good indicator for sexual preference in female zebra finches. *Ethol Ecol Evol*. 18:195–204.
- Witte K, Caspers B. 2006. Sexual imprinting on a novel blue ornament in zebra finches. *Behaviour*. 143:969–991.
- Witte K, Noltemeier B. 2002. The role of information in mate-choice copying in female sailfin mollies (*Poecilia latipinna*). *Behav Ecol Sociobiol*. 52:194–202.
- Witte K, Sawka K. 2003. Sexual imprinting on a novel trait in the dimorphic zebra finch: sexes differ. *Anim Behav*. 65:195–203.
- Witte K, Ueding K. 2003. Sailfin molly females (*Poecilia latipinna*) copy the rejection of a male. *Behav Ecol*. 3:389–395.
- Wolters HE. 1979–1982. *Die Vogelarten der Erde*. Hamburg (Germany): Parey Verlag.
- Zahavi A, Zahavi A. 1997. *The handicap principle, a missing piece of Darwin's puzzle*. Oxford: Oxford University Press.
- Zann RA. 1996. *The zebra finch: a synthesis of field and laboratory studies*. Oxford: Oxford University Press.