

# The role of the model in mate-choice copying in female zebra finches

Nina Kniel  | Katharina Müller | Klaudia Witte

Research Group of Ecology and Behavioral Biology, Institute of Biology, Department of Chemistry and Biology, University of Siegen, Siegen, Germany

**Correspondence**

Nina Kniel, Research Group of Ecology and Behavioral Biology, Institute of Biology, Department of Chemistry and Biology, University of Siegen, Siegen, Germany.  
Email: kniel@biologie.uni-siegen.de

**Funding information**

University of Siegen

Editor: L. Fusani

**Abstract**

Previous studies have shown that zebra finch females copy the mate choice of other females by choosing a mate of the same phenotype as the one chosen by another female (model). Little is known about the influence of the model female on the mate choice of the observing female. Therefore, we investigated the role of the model female in mate-choice copying by manipulating her phenotype. Test females could choose between an unadorned male and an artificially adorned male, that is, wearing a red feather on the forehead. During a 2h observation period, test females could observe a single male in one cage and a male–female pair in another cage. In treatment one, the single male was unadorned and both the male and the female of the pair (model female) were adorned. In treatment two, the single male was adorned, the male of the pair unadorned and the model female adorned. Afterwards, test females could again choose between two new males, one adorned and one unadorned. In treatment one, test females first showed no preference for one of the two males, but avoided adorned males after the observation period. In treatment two, test females lost an initial preference for unadorned males after the observation period. In both treatments, test females did not copy the mate choice of the adorned model female. Adorned model females seemed to have a negative influence on the attractiveness of their mates' phenotype. Test females might have recognised model females as females of a different phenotype within their species which are adapted to different environmental conditions, or even have recognised model females as a female of another species. Our study demonstrates the important role of the model female in the complex public information network in zebra finches.

**KEYWORDS**

artificial, ornamentation, mate-choice copying, public information, zebra finch

## 1 | INTRODUCTION

Public information is information inadvertently created by individuals and can give information about the performance of those individuals (Danchin, Giraldeau, Valone, & Wagner, 2004). The opportunity to observe other conspecifics and the possibility to use public information may especially occur in group living species (Dall, Giraldeau, Olsson, McNamar, & Stephens, 2005; Danchin et al., 2004; Ioannou, Couzin, James, Croft, & Krause, 2011; Valone, 2007; Valone & Templeton,

2002). The use of public information in mate choice has been recognised as a meaningful mechanism for the cultural transmission of mate preferences (overviews in Vakirtzis, 2011; Witte, Kniel, & Kureck, 2015). One form of using public information in mate choice is called mate-choice copying (Westneat, Walters, McCarthy, Hatch, & Hein, 2000; Witte, 2006a). Individuals copy the mate choice of others by observing a sexual interaction between a female and a male, and afterwards copulate with the same potential partner, or reject him or her, as the observed individual did before (Witte & Ueding, 2003). Several

studies have found evidence of this mate-choice strategy in different species (overviews in Vakirtzis, 2011; Witte et al., 2015). Individuals may not only copy the choice for individual potential mates, but they may generalise and prefer other potential mates of the same phenotype as the observed one chosen as a mate as well (Godin, Herdmann, & Dugatkin, 2005; Kniel, Schmitz, & Witte, 2015; Kniel, Dürler, et al., 2015; Witte & Noltemeier, 2002).

One interesting aspect in the context of using public information is the role of the model individual. The role of a model, which is another conspecific interacting with the environment and/or conspecifics, in social learning has been investigated in numerous contexts, such as feeding (Benskin, Mann, Lachlan, & Slater, 2002; Galef, Kennet, & Wigmore, 1984; Galef, Rudolf, & Whiskin, 1998; Guillette & Healy, 2014; Katz & Lachlan, 2003; Lachlan, Crooks, & Laland, 1998; Nicol & Pope, 1994, 1999; Swaney, Kendal, Capon, Brown, & Laland, 2001; Valsecchi, Choleris, Moles, Guo, & Mainardi, 1996), or song learning (Böhner, 1983; Clayton, 1987; Payne, 1985).

In mate-choice copying, the identity of the model seems to be important. The observing female receives information about the quality of the male by his interaction with the model female. Dugatkin and Godin (1993) found that young female guppies are much more likely to copy the mate choice of older, more experienced females than vice versa (see also Vukomanovic & Rodd, 2007). Further, Amlacher and Dugatkin (2005) found that young female guppies do not copy other females randomly, but that they rather copy older females if given the opportunity to observe a younger and an older female. In sailfin mollies (*Poecilia latipinna*), Hill and Ryan (2006) found that females copied the choice of their conspecifics while avoiding males associated with another heterospecific female, the gynogenetic hybrid species, the Amazon molly (*P. formosa*). When different female phenotypes within a species exist, it might be that females of the one phenotype (here adorned) are adapted to a different environment than females of the other phenotype (here unadorned) and thus might show a different mate preference. Copying the choice of a female of a different phenotype might therefore not be adaptive. Thus, we expected that the phenotype of the model female will matter in mate-choice copying in female zebra finches and investigated the influence of the model female, that is, her phenotype, on mate-choice copying in female zebra finches. We asked whether female zebra finches would copy the mate choice of a conspecific model female, which was artificially adorned with a red feather on the forehead, thus expressing a different phenotype as the test females. Female zebra finches are known to copy the mate choice of their wild-type conspecific females (Swaddle, Cathey, Correll, & Hodkinson, 2005; Drullion & Dubois, 2008; Kniel, Dürler, et al., 2015; Kniel, Schmitz, et al., 2015; but see Doucet, Yezerinac, & Montgomerie, 2004). As Benskin et al. (2002) found that both sexes of the zebra finch preferentially copied individuals wearing red leg bands over those with green leg bands in a feeding context, we hypothesised that the phenotype of the model female in mate-choice copying might also be of importance. In our experiments, we gave females the choice between two males, one artificially adorned with a red feather, one unadorned. Then, females could gain public information in two situations. In treatment

one, females could observe a single unadorned male in one cage and a male–female pair of mated and adorned zebra finches in another cage. In treatment two, females could observe a single adorned male in one cage and a male–female pair of mated zebra finches, where the male was unadorned and the model female adorned, in another cage. Afterwards, females could again choose between new males of the two phenotypes. As we used the same experimental set-up and procedure, including the red feather as an adornment, as in Kniel, Dürler, et al. (2015), we could compare our results to those mate-choice copying experiments in which the model females' phenotype was not manipulated.

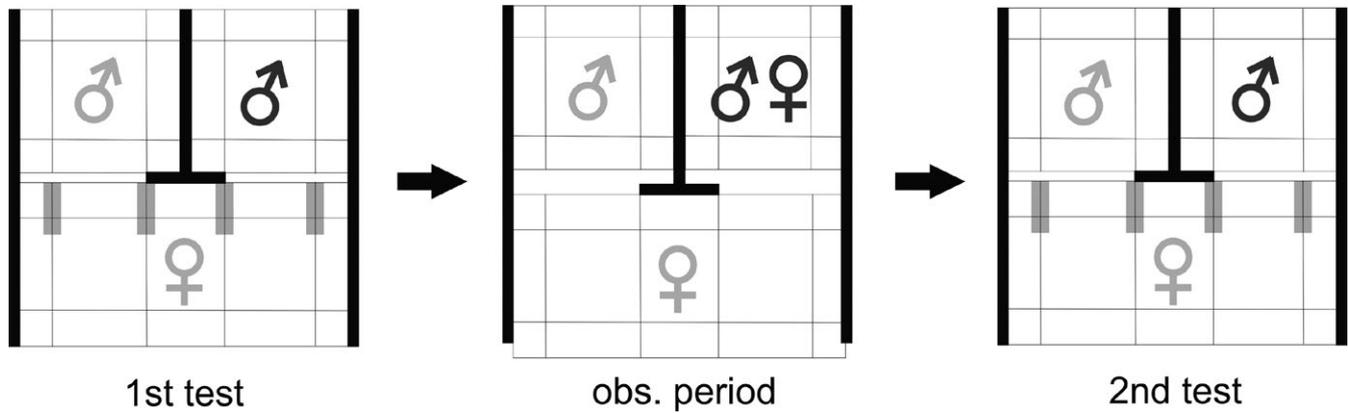
## 2 | METHODS

### 2.1 | Study species

Test and stimulus birds were sexually mature  $F_{8-11}$  descendants (females: mean age approximately 31 months, minimum: 8 months, maximum: 46 months; males: mean age approximately 30 months, minimum: 8 months, maximum: 44 months) of wild zebra finches that were exported from Northern Victoria, Australia, in 1992 (Meyer T, pers. comm.). Birds from all age classes were equally used as test as well as stimulus birds, and both sexually experienced and sexually inexperienced test females were used. They were kept in six aviaries (length x width x height: four aviaries:  $2 \times 1.65 \times 2.30 \text{ m}^3$  and two aviaries:  $2.25 \times 1.05 \times 2.30 \text{ m}^3$ ), separated by sex after maturation (mean 71, minimum 56 and maximum 92 days after hatching) for at least 6 months before we used them in the experiments. The air-conditioned room ( $6.80 \times 4 \times 2.40 \text{ m}^3$ ) (Temperature =  $24^\circ \pm 1^\circ\text{C}$ , Humidity =  $60\% \pm 10\%$ ) with windows at two sides was illuminated with fluorescent lighting including UV-range at a 14:10h light:dark photoperiod. Both sexes wore numbered orange or white leg bands, or silver metal leg bands (neutral in zebra finch mate choice; Burley, Krantzberg, & Radman, 1982; Burley, 1985a,b). Each aviary contained several branches, coconut fibres for nest building, several nest-boxes, and sand, food and water 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.

### 2.2 | Experimental set-up

Experiments were conducted in May and June 2015 by a single person (K. M.) in an air-conditioned ( $T = 24 \pm 1^\circ\text{C}$ ,  $H = 60 \pm \text{max } 10\%$ ) experimental room ( $4.20 \times 2.10 \times 2.30 \text{ m}^3$ ) without windows, which was illuminated with fluorescent lighting including UV range at a 14:10h light:dark photoperiod. Experiments were performed in cages, consisting of a wooden frame with green wire mesh as "walls" (mesh width 1.2 cm). Stimulus birds (each cage:  $49 \times 43 \times 50 \text{ cm}^3$ ) were placed side by side, and the test bird (cage:  $97 \times 43 \times 52 \text{ cm}^3$ ) was placed in front of them (Figure 1). Each cage contained water, food and sand ad libitum in little bowls on the ground and four perches: one low perch parallel and near to the front (10 cm above the bottom



**FIGURE 1** Experimental set-up for female mate-choice tests (example for treatment one), top-view. 1st test = first mate-choice test, obs. period = observation period, 2nd test = second mate-choice test. Grey male/female symbols = unadorned/wild-type, black male/female symbols = adorned. Grey areas are mate-choice zones. Thin lines are perches, and bold lines are screens

of the cage), one high perch parallel and near to the backside (35 cm), and two additional perches parallel and near to the side of the cage in middle height (20 cm). The larger test bird cage had two additional perches of choice in middle height. Several wooden screens, placed between the stimulus cages, and around the whole set-up, prevented visual contact between the stimulus birds before starting the tests and between the phases of a test. 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 or stimulus cages at least 15 hours before we started the experiments the next morning in visual but not acoustic isolation from other birds. Stimulus birds were either artificially adorned with a red feather, standing upright like a crest and representing a conspicuous trait, or equipped with a piece of a grey flat flight feather (unadorned), representing the common phenotype, when they were caught. Red feathers were cut out of a red feather boa along the quill (length: 2 cm, width: 4–5 mm). Grey flight feathers were cut to triangles (maximum edge length 5 mm). Both were glued to the forehead with double-sided tape onto the natural forehead feathers of stimulus birds. Feathers, as well as pieces of flight feathers, could easily be removed afterwards. This way, all stimulus and model birds were handled equally and not harmed in any way, but differed in their visible adornment. This method was successfully used before in a number of experiments with zebra finches (Kniel, Bender, & Witte, 2016; Kniel, Dürler, et al., 2015; Kniel, Schmitz, et al., 2015; Witte & Caspers, 2006; Witte & Sawka, 2003) and the Javanese mannikin *Lonchura leucogastroides* (Plenge, Curio, & Witte, 2000; Witte & Curio, 1999; Witte, Hirschler, & Curio, 2000).

### 2.3 | Procedure

In the first mate-choice test, test females could choose between an artificially adorned (red feather) and an unadorned stimulus male to determine the initial mate preference and to test whether test females

had a latent, that is, genetically determined, preference for a novel phenotype in males. During the observation period, which lasted 2h, test females could observe new stimulus males in two different situations. In treatment one, one cage contained a single unadorned male and the other contained a pair of zebra finches that were both artificially adorned with a red feather, the model female and her mate. In treatment two, one cage contained a single adorned male and the other contained a pair of zebra finches where the model female was adorned and her mate was unadorned. The respective pairs were taken from their breeding cages and transferred to the stimulus cage. They had been paired for several months and had reproduced with each other. After this observation period, test females again got the opportunity to choose between two new stimulus males, one adorned and one unadorned (second mate-choice test). Between the different phases, we gave all birds the time to acclimate for up to five minutes, which is sufficient for birds to calm down (Witte & Caspers, 2006; Witte & Sawka, 2003). We exchanged stimulus males between each phase because we wanted to test whether females generalise and prefer the observed male phenotype instead of preferring the same individual male.

By removing the screens that prevented the test females from seeing the stimulus males, we started the first mate-choice test, which lasted  $2 \times 20$  min with a switch of stimulus males' cages after the first 20 min to control for side biases. We measured the time [s] the test females spent perching on the outer one-third of the perches of choice adjacent to the stimulus males (mate-choice zone; grey area in Figure 1) every 10 s. If the test females changed position during the 10-s interval, 5 s was 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 (Kniel, Dürler, et al., 2015; Kniel, Schmitz, et al., 2015; Kniel et al., 2016; Witte, 2006b; Witte & Caspers, 2006; Witte & Sawka, 2003). From this time, we also calculated the choosing motivation (total time spent in both mate-choice zones during the

2 × 20 min mate-choice test). Additionally, we measured the time that the respective stimulus males spent in the front on their cage (outer one-third of the perches close to the test females) and we counted the number of courtship displays (whether or not males sang within a 10-s interval, either directed at females or undirected). Male song rate is known to influence female mate choice as females spend more time with males that sing more often compared to those that sing less often (Forstmeier & Birkhead, 2004). During the observation period, the side where the pair was presented was randomised. The second mate-choice test was performed like the first mate-choice test, but again with new stimulus males. After each test, we measured the body weight of all birds and placed them back into their aviaries or cages. We used each test female only once as a test bird. Due to the limited amount of birds available for experiments, we reused stimulus males for up to four mate-choice tests, but always in combination with different stimulus males and both as an adorned or an unadorned male. Test females were not closely related to the respective stimulus males, including the presented pairs. Pair mates were not used within the same test; that is, a test female was not tested with its mate as stimulus male. We tested a total number of 16 females in treatment one and 15 females in treatment two.

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 (individuals not known to the test and stimulus birds; recorded in the aviary room in 2008) through a loudspeaker (Speed Link, Brave 2.0 Stereo Sound System). As 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, approximately 30 cm away from the table on which we placed the test females. The sound was played at approximately 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 females that showed side biases during the first mate-choice test, that is, those that spent more than 80% of their choosing time on the same side, even though we had switched the position of the stimulus cages, were excluded from the analysis in accordance with other studies (Dosen & Montgomerie, 2004; Hoysak & Godin, 2007; Kniel, Dürler, et al., 2015; Kniel, Schmitz, et al., 2015; Kniel et al., 2016; Schlupp & Ryan, 1997; Williams & Mendelson, 2010).

Behavioural experiments were performed under the permission of the County Veterinary Office, Siegen, Germany (permit numbers: 53.6 55-05).

## 2.4 | Analysis

We analysed choosing motivation of test females with a Wilcoxon test. We analysed test females' mate choice using mate-choice scores of time spent with the artificially adorned males (time spent with the adorned male/time spent with both the adorned and the unadorned male). To test whether test females showed a preference for one of the two stimulus males within a mate-choice test, we tested the mate-choice scores of time spent with adorned males against a 50%

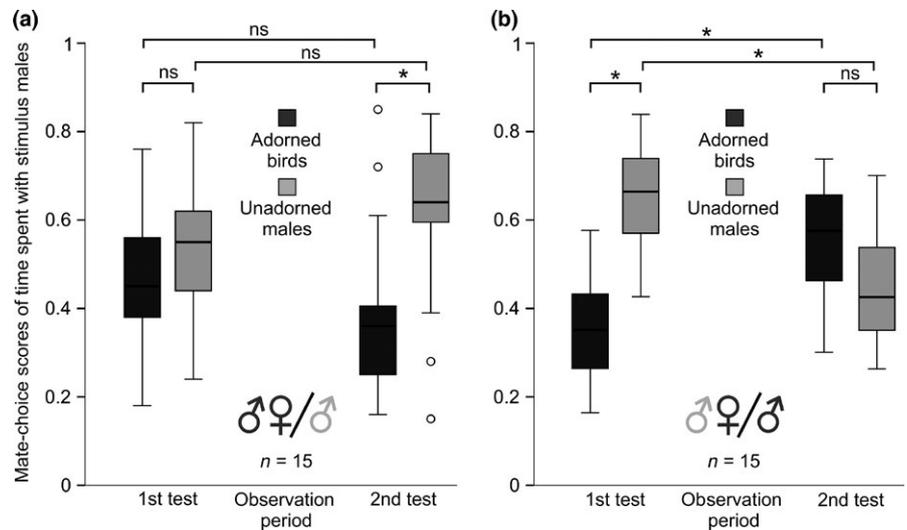
expectation using a one-sample *t* test. To test whether mate-choice scores of time spent changed between the mate-choice tests, that is, whether the change of time spent was influenced by test number, we transformed mate-choice scores via arcsine square root to have normally distributed data and used a repeated-measures ANOVA (RMANOVA) (with mate-choice test as within-subject factor). To compare number of intervals with song of stimulus males and time of stimulus males spent close to the test females, we used a Mann–Whitney U test. To compare weight, we used an unpaired *t* test. For time spent, male singing activity and weight, we give the median as well as the first and third quartile in parentheses. Statistical analyses were carried out using SPSS (IBM SPSS Statistics 23). Significance levels were set at  $\alpha = 0.05$ . All *p*-values are two-tailed.

## 3 | RESULTS

### 3.1 | Treatment one

In treatment one, one experiment was cancelled because the mate of the test female was accidentally used as a stimulus male. Three test females showed a side bias and were retested once successfully. This left a total number of 15 females. Choosing motivation did not change between the two mate-choice tests (Wilcoxon test:  $U = -0.341$ ,  $n = 15$ ,  $p = .733$ ). Mate-choice scores of time spent with adorned males were not affected by test number (RMANOVA:  $F_{1,14} = 1.588$ ,  $p = .228$ , Figure 2a). Females showed no preference for one of the two males during the first mate-choice test (one-sample *t* test:  $t = -0.871$ ,  $df = 14$ ,  $p = .398$ ), but they showed a preference for unadorned males during the second mate-choice test (one-sample *t* test:  $t = -2.147$ ,  $df = 14$ ,  $p = .050$ ). They spent 545 s (230 s, 717.4 s) with adorned males and 595 s (367.5 s, 875 s) with unadorned males in the first mate-choice test, and 365 s (267.5 s, 647.5 s) with adorned males and 795 s (282.5 s, 1182.5 s) with unadorned males during the second mate-choice test. Adorned and unadorned stimulus males did not differ in time spent close to test females during the first (Mann–Whitney U test:  $U = -0.913$ ,  $n_1 = n_2 = 15$ ,  $p = .361$ ) and the second mate-choice test (Mann–Whitney U test:  $U = -0.290$ ,  $n_1 = n_2 = 15$ ,  $p = .772$ ). During the first mate-choice test, adorned males spent 670 s (445 s, 1020 s) with test females and unadorned males 1180 s (485 s, 1355 s). During the second mate-choice test, adorned males spent 965 s (602.5 s, 1527.5 s) with test females and unadorned males 1315 s (725 s, 1475 s). Adorned males sang more often than unadorned males during the first mate-choice test (Mann–Whitney U test:  $U = -2.580$ ,  $n_1 = n_2 = 15$ ,  $p = .010$ ), but not during the second mate-choice test (Mann–Whitney U test:  $U = -0.689$ ,  $n_1 = n_2 = 15$ ,  $p = .491$ ). During the first mate-choice test, adorned males sang 14 times (4, 22) and unadorned males 3 times (2, 5.5), and during the second mate-choice test, adorned males sang 4 times (3, 12.5) and unadorned males 3 times (2, 11). Test females were of the same weight as model females (unpaired *t* test:  $T = 0.487$ ,  $df = 28$ ,  $p = .630$ ). Test females weighed a median of 10.47 g (10.35 g, 11.12 g) and model females 10.33 g (10.23 g, 10.88 g). Adorned and unadorned males did not differ in weight during the first mate-choice test (unpaired *t* test:

**FIGURE 2** Mate-choice copying experiments: (a) treatment one and (b) treatment two. 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 males. 1st test = first mate-choice test, 2nd test = second mate-choice test. Grey male symbols = unadorned and black male/female symbols = adorned. \* $p < .05$ , ns = not significant



$T = 1.638$ ,  $df = 28$ ,  $p = .113$ ), the observation period (unpaired  $t$  test:  $T = -1.045$ ,  $df = 28$ ,  $p = .305$ ) and the second mate-choice test (unpaired  $t$  test:  $T = 0.957$ ,  $df = 28$ ,  $p = .347$ ). In the first mate-choice test, adorned males weighed 10.98 g (10.62 g, 11.89 g) and unadorned males 10.89 g (9.98 g, 11.15 g). In the observation period, adorned males weighed 10.50 g (10.31 g, 11.2 g) and unadorned males 11.15 g (10.36 g, 11.54 g). In the second mate-choice test, adorned males weighed 10.78 g (10.59 g, 11.47 g) and unadorned males 10.60 g (9.97 g, 11.20 g).

### 3.2 | Treatment two

In treatment two, one female was retested successfully because of a side bias, which resulted in a total number of 15 females tested. Choosing motivation did not change between the two mate-choice tests (Wilcoxon test:  $U = -0.625$ ,  $n = 15$ ,  $p = .256$ ). Mate-choice scores of time spent with adorned males were affected by test number (RMANOVA:  $F_{1,14} = 17.001$ ,  $p = .001$ , Figure 2b). Their time spent with adorned males increased, whereas their time spent with unadorned males decreased. Females showed a preference for unadorned males during the first mate-choice test (one-sample  $t$  test:  $t = -4.573$ ,  $df = 14$ ,  $p < .001$ ), but not during the second mate-choice test (one-sample  $t$  test:  $t = 1.677$ ,  $df = 14$ ,  $p = .116$ ). They spent 415 s (307.5 s, 510 s) with adorned males and 625 s (447.5 s, 920 s) with unadorned males in the first mate-choice test, and 630 s (527.5 s, 750 s) with adorned and 530 s (347.5 s, 675 s) with unadorned males during the second mate-choice test. Adorned and unadorned stimulus males did not differ in time spent close to test females during the first (Mann-Whitney U test:  $U = -0.207$ ,  $n_1 = n_2 = 15$ ,  $p = .836$ ) and the second mate-choice test (Mann-Whitney U test:  $U = -0.373$ ,  $n_1 = n_2 = 15$ ,  $p = .709$ ). During the first mate-choice test, adorned males spent 985 s (677.5 s, 1502.5 s) with test females and unadorned males 1070 s (757.5 s, 1382.5 s). During the second mate-choice test, adorned males spent 1095 s (720 s, 1347.5 s) with test females and unadorned males 785 s (440 s, 1280 s). Males did also not differ in their singing activity during the first (Mann-Whitney U test:  $U = -1.293$ ,  $n_1 = n_2$

$= 15$ ,  $p = .196$ ) and second mate-choice test (Mann-Whitney U test:  $U = -0.751$ ,  $n_1 = n_2 = 15$ ,  $p = .453$ ). During the first mate-choice test, adorned males sang 5 times (2, 8) and unadorned males 13 times (1.5, 20.5), and during the second mate-choice test, adorned males sang 4 times (1.5, 10) and unadorned males 7 times (3, 9.5). Test females were of the same weight as model females (unpaired  $t$  test:  $T = 1.238$ ,  $df = 28$ ,  $p = .226$ ). Test females weighed a median of 10.89 g (10.22 g, 11.02 g) and model females 10.31 g (10.23 g, 10.72 g). Adorned and unadorned males did not differ in weight during the first mate-choice test (unpaired  $t$  test:  $T = -0.295$ ,  $df = 28$ ,  $p = .770$ ), the observation period (unpaired  $t$  test:  $T = 0.658$ ,  $df = 28$ ,  $p = .516$ ) and the second mate-choice test (unpaired  $t$  test:  $T = -1.015$ ,  $df = 28$ ,  $p = .319$ ). In the first mate-choice test, adorned males weighed 10.94 g (10.34 g, 11.22 g) and unadorned males 10.76 g (10.71 g, 11.92 g). In the observation period, adorned males weighed 10.60 g (10.22 g, 11.29 g) and unadorned males 10.59 g (10.34 g, 11.05 g). In the second mate-choice test, adorned males weighed 10.76 g (10.30 g, 11.19 g) and unadorned males 11.04 g (10.50 g, 11.37 g).

## 4 | DISCUSSION

In the present study, we investigated whether the phenotype of a model female matters in mate-choice copying in female zebra finches. In contrast to all previous studies on mate-choice copying in zebra finches and in most other species (for overviews see Vakirtzis, 2011; Witte et al., 2015), we changed the phenotype of the model female and tested whether wild-type zebra finch females would copy the mate choice of females of a different artificial phenotype (a red feather on the forehead) in two treatments. In treatment one, test females first showed no preference for one of the males, but they preferred unadorned males over artificially adorned males after the observation period, in which they observed an adorned model female with her adorned mate. In treatment two, test females lost an initial preference for unadorned males after they had observed an adorned model female with her unadorned mate, and showed a significant

change between the two mate-choice tests. Thus, in both treatments, test females did not copy the mate choice of the model female, that is, did not prefer a male of the same phenotype as the model female's mate.

These results are in contrast to previous findings (Kniel, Dürler, et al., 2015), where zebra finch females copied the mate choice of the model females and preferred the male of the phenotype (artificially adorned with a red feather) that the model female had chosen. Their experiment was carried out with birds of the same population and under the same conditions in 2009. We therefore compared females' mate choice after they had obtained public information (their mate choice scores for artificially adorned males during the second mate-choice test) in this study with the results of the mate-choice copying experiment in Kniel, Dürler, et al. (2015), where the model females of the pairs were not adorned. In both our treatments, females' choices for adorned males were highly different from those in Kniel, Dürler, et al. (2015) where females showed mate-choice copying (treatment one: unpaired  $t$  test:  $t = 5.014$ ,  $df = 37$ ,  $p < .001$ ; treatment two: unpaired  $t$  test:  $t = 2.765$ ,  $df = 37$ ,  $p = .009$ ). As we know that female zebra finches copy the mate choice for artificially adorned males (Kniel, Dürler, et al., 2015; Kniel, Schmitz, et al., 2015), the absence of copying in this experiment was due to the manipulated phenotype of the model female.

One explanation for the lack of mate-choice copying could be the colour of the feather used in this study. As red is a more male-specific colour in zebra finches, test females might have recognised model females as more male-like and therefore it would not make sense to copy their choice. As our females showed no change in choosing motivation between the two mate-choice tests in both treatments, a change in preference cannot be due to a general loss of motivation to spent time with the respective males. Other factors like the time stimulus males spent with the test females, stimulus male singing activity, or weight of the respective birds, could also not explain our results.

In our experiments, test females avoided males of the same phenotype as the ones they had seen interacting with the adorned model female. It could be that wild-type females recognised adorned females as females of a different phenotype within their species which are adapted to different environmental conditions and have, therefore, developed different preferences in mate choice which might not be advantageous for females of the wild-type phenotype. Copying the choice of a female of a different phenotype might, therefore, not be adaptive. Test females might even have recognised model females as a female of another species; that is, the observed effects could have arisen from mechanisms that evolved in the context of species recognition. Encountering an adorned pair might have triggered such mechanisms, as heterospecifics can, for example, be recognised as another species by their tendency to mate assortatively. In that case, avoiding males chosen by those females would make absolute sense, as consequently males chosen by females of another species might also be males of another species, and pairing with them will lead to hybridisation. A mixed pair (adorned female with unadorned male), however, might indicate that there is no barrier between the two types, that is, unadorned

males and previously rejected adorned males, making the two males equally suitable as potential partners. Such an explanation would be in line with a study in sailfin mollies, in which Hill and Ryan (2006) found that females copied the choice of their conspecifics while avoiding males associated with another heterospecific female, the gynogenetic hybrid species, the Amazon molly. This could be an explanation for the preference for unadorned males in the second mate-choice test of treatment one.

Our findings demonstrate the importance of the role of the model female in mate-choice copying in female zebra finches, especially that her phenotype matters. The mate preference of a conspecific female of the "wrong" phenotype can even lead females to reject the common and previously preferred male phenotype. This highlights the important role of the model female in the complex public information network.

## ACKNOWLEDGEMENTS

This work was supported by the "Hochschulinterne Forschungsförderung (HIFF)" of the University of Siegen. Nina Kniel was supported by a PhD scholarship of the University of Siegen. We thank two anonymous referees for helpful comments on a previous version.

## REFERENCES

- Amlacher, J., & Dugatkin, L. A. (2005). Preference for older over younger models during mate-choice copying in young guppies. *Ethology Ecology & Evolution*, 17, 161–169.
- Benskin, C. M. H., Mann, N. I., Lachlan, R. F. & Slater, P. J. B. (2002). Social learning directs feeding preferences in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, 64, 823–828.
- Böhner, J. (1983). Song learning in the zebra finch (*Taeniopygia guttata*): Selectivity in the choice of a tutor and accuracy of song copies. *Animal Behaviour*, 31, 231–237.
- Burley, N. (1985a). Leg-band and mortality patterns of captive breeding populations of zebra finches. *The Auk*, 102, 647–651.
- Burley, N. (1985b). The organization of behaviour and the evolution of sexually selected traits. In P. A. Gowaty & D. W. Mock (Eds.), *Avian Monogamy* (pp. 22–44). Washington, DC: American Ornithologists Union.
- Burley, N., Krantzberg, G., & Radman, P. (1982). Influence of colour-banding on the conspecific preferences of zebra finches. *Animal Behaviour*, 30, 444–455.
- Clayton, N. S. (1987). Song tutor choice in zebra finches. *Animal Behaviour*, 35, 714–721.
- Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamar, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20, 187–193.
- Danchin, E., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science*, 305, 487–491.
- Dosen, L. D., & Montgomerie, R. (2004). Female size influences mate preferences of male guppies. *Ethology*, 110, 245–255.
- 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.
- Drullion, D., & Dubois, F. (2008). Mate-choice copying by female zebra finches, *Taeniopygia guttata*: What happens when model females provide inconsistent information? *Behavioral Ecology and Sociobiology*, 63, 269–276.

- Dugatkin, L. A., & Godin, J.-G. J. (1993). Female mate copying in the guppy (*Poecilia reticulata*): Age-dependent effects. *Behavioral Ecology*, 4, 289–292.
- Forstmeier, W., & Birkhead, T. R. (2004). Repeatability of mate choice in the zebra finch: Consistency within and between females. *Animal Behaviour*, 68, 1017–1028.
- Galef, B. G. Jr, Kennet, D. J., & Wigmore, S. W. (1984). Transfer of information concerning distant foods in rats: A robust phenomenon. *Animal Learning & Behavior*, 12, 292–296.
- Galef, B. G. Jr, Rudolf, B., & Whiskin, E. E. (1998). Familiarity and relatedness: Effects on social learning about foods by Norway rats and Mongolian gerbils. *Animal Learning & Behavior*, 26, 448–454.
- Godin, J.-G. J., Herdmann, 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.
- Guillette, L. M., & Healy, S. D. (2014). Mechanisms of copying behaviour in zebra finches. *Behavioural Processes*, 108, 177–182.
- Hill, S. E., & Ryan, M. J. (2006). The role of model female quality in the mate choice copying behaviour of sailfin mollies. *Biology Letters*, 2, 203–205.
- Hoysak, D. J., & Godin, J.-G. Jr (2007). Repeatability of male mate choice in the mosquitofish, *Gambusia holbrooki*. *Ethology*, 113, 1007–1018.
- Ioannou, C. C., Couzin, I. D., James, R., Croft, D. P., & Krause, J. (2011). Social organisation and information transfer in schooling fish. In C. Brown, K. Laland, & J. Krause (Eds.), *Fish Cognition and Behavior* (pp. 217–239). New York: Wiley-Blackwell.
- Katz, M., & Lachlan, R. F. (2003). Social learning of food types in zebra finches (*Taenopygia guttata*) is directed by demonstrator sex and feeding activity. *Animal Cognition*, 6, 11–16.
- Kniel, N., Bender, S., & Witte, K. (2016). Sex-specific audience effect in the context of mate choice in zebra finches. *PLoS ONE*, 11(2), e0147130. doi:10.1371/journal.pone.0147130
- Kniel, N., Dürler, C., Hecht, I., Heinbach, V., Zimmermann, L., & Witte, K. (2015). Novel mate preference through mate-choice copying in zebra finches: Sexes differ. *Behavioral Ecology*, 26, 647–655.
- Kniel, N., Schmitz, J., & Witte, K. (2015). Quality of public information matters in mate-choice copying in female zebra finches. *Frontiers in Zoology*, 12. doi: 10.1186/s12983-015-0119-8
- Lachlan, R. F., Crooks, L., & Laland, K. N. (1998). Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, 56, 181–190.
- Nicol, C. J., & Pope, S. J. (1994). Social learning in small flocks of laying hens. *Animal Behaviour*, 47, 1289–1296.
- Nicol, C. J., & Pope, S. J. (1999). The effects of demonstrator social status and prior foraging success on social learning in laying hens. *Animal Behaviour*, 57, 163–171.
- Payne, R. B. (1985). Behavioral continuity and change in local song populations Village indigobirds *Vidua chalybeata*. *Zeitschrift für Tierpsychologie*, 70, 1–44.
- Plenge, M., Curio, E., & Witte, K. (2000). Sexual imprinting supports the evolution of novel male traits by transference of a preference for the colour red. *Behaviour*, 137, 741–758.
- Schlupp, I., & Ryan, M. J. (1997). Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males. *Behavioral Ecology*, 8, 104–107.
- 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, Series B: Biological Sciences*, 272, 1053–1058.
- Swaney, W., Kendal, J., Capon, H., Brown, C., & Laland, K. N. (2001). Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, 62, 591–598.
- Vakirtzis, A. (2011). Mate choice copying and nonindependent mate choice: A critical review. *Annales Zoologici Fennici*, 48, 91–107.
- Valone, T. J. (2007). From eavesdropping on performance to copying the behavior of others: A review of public information use. *Behavioral Ecology and Sociobiology*, 62, 1–14.
- Valone, T. J., & Templeton, J. J. (2002). Public information for the assessment of quality: A widespread social phenomenon. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 357, 1549–1557.
- Valsecchi, P., Choleris, E., Moles, A., Guo, G., & Mainardi, M. (1996). Kinship and familiarity as factors affecting social transfer of food preferences in adult Mongolian gerbils (*Meriones unguiculatus*). *Journal of Comparative Psychology*, 110, 243–251.
- Vukomanovic, J., & Rodd, F. H. (2007). Size-dependent female mate copying in the guppy (*Poecilia reticulata*): Large females are role models but small ones are not. *Ethology*, 113, 579–586.
- 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.
- Williams, T. H., & Mendelson, T. C. (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 C. Brown, K. Laland, & J. Krause (Eds.), *Fish Cognition and Behavior* (pp. 70–95). New York: Wiley-Blackwell.
- Witte, K. (2006b). Time spent is a good indicator for sexual preference in female zebra finches. *Ethology Ecology & Evolution*, 18, 195–204.
- Witte, K., & Caspers, B. (2006). Sexual imprinting on a novel blue ornament in zebra finches. *Behaviour*, 143, 969–991.
- Witte, K., & Curio, E. (1999). Sexes of a monomorphic species differ in preference for mates with a novel trait. *Behavioral Ecology*, 10, 15–21.
- Witte, K., Hirschler, U., & Curio, E. (2000). Sexual imprinting on a novel adornment influences mate preferences in the Javanese Mannikin *Lonchura leucogastroides*. *Ethology*, 106, 349–363.
- Witte, K., Kniel, N., & Kureck, I. M. (2015). Mate-choice copying: Status quo and where to go. *Current Zoology*, 61, 1073–1081.
- Witte, K., & Noltemeier, B. (2002). The role of information in mate-choice copying in female sailfin mollies (*Poecilia latipinna*). *Behavioral Ecology and Sociobiology*, 52, 194–202.
- Witte, K., & Sawka, N. (2003). Sexual imprinting on a novel trait in the dimorphic zebra finch: Sexes differ. *Animal Behaviour*, 65, 195–203.
- Witte, K., & Ueding, K. (2003). Sailfin molly females copy the rejection of a male. *Behavioral Ecology*, 14, 389–395.

**How to cite this article:** Kniel N, Müller K, Witte K. The role of the model in mate-choice copying in female zebra finches. *Ethology*. 2017;00:1–7. <https://doi.org/10.1111/eth.12611>