Journal of Comparative Psychology
2016, Vol. 130, No. 1, 36–43

© 2016 American Psychological Association
0735-7036/16/$12.00 http://dx.doi.org/10.1037/a0040027

Mate Call as Reward: Acoustic Communication Signals Can Acquire Positive Reinforcing Values During Adulthood in Female Zebra Finches (*Taeniopygia guttata*)

Alexandra M. Hernandez, Emilie C. Perez, Hervé Mulard, Nicolas Mathevon, and Clémentine Vignal
Université de Lyon/Saint-Etienne

Social stimuli can have rewarding properties and promote learning. In birds, conspecific vocalizations like song can act as a reinforcer, and specific song variants can acquire particular rewarding values during early life exposure. Here we ask if, during adulthood, an acoustic signal simpler and shorter than song can become a reward for a female songbird because of its particular social value. Using an operant choice apparatus, we showed that female zebra finches display a preferential response toward their mate's calls. This reinforcing value of mate's calls could be involved in the maintenance of the monogamous pair-bond of the zebra finch.

Keywords: songbird, reinforcement, operant conditioning, mate preference, pair-bond

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Social stimuli, such as social contact or social interactions, show rewarding properties in several species (Trezza, Campolongo, & Vanderschuren, 2011). Individuals will seek exposure to these social stimuli, which can be used as a reward in learning tasks. For instance, rats can learn a T maze task for the opportunity to interact with a conspecific (Humphreys & Einon, 1981; Normansell & Panksepp, 1990; Taylor, 1981). Social interactions can also be used as reinforcers in protocols of conditioned place preference, where rodents show an acquired preference for a cage compartment previously associated with social interactions (Douglas, Varlinskaya, & Spear, 2004; Gil, Nguyen, McDonald, & Albers, 2013; Tzschentke, 2007). Social play is highly rewarding in young mammals, like rats or primates, and can be used as an incentive in several learning situations, like maze or lever pressing (Humphreys & Einon, 1981; Ikemoto & Panksepp, 1992; Normansell & Panksepp, 1990), and maternal mammals find juveniles reinforcing, for example, pressing for pups in an operant task (Lee, Clancy, & Fleming, 1999).

Social stimuli reduced to only one sensory modality can still be rewarding. Visual stimuli with a social content can act as positive reinforcers in operant tasks for monkeys (Blatter & Schultz, 2006; Brannon, Andrews, & Rosenblum, 2004; Deaner, Khera, & Platt, 2005). The sight of conspecifics is also rewarding in several fish species (Al-Imari & Gerlai, 2008; Gerlai & Hogan, 1992; Rnic, 1977; Thompson, 1963) or in roosters (Thompson, 1964). Similar studies have shown that social odors may act as reinforcers, for example, in newborn European rabbits (*Oryctolagus cuniculus*; Coureaud et al., 2006) and in rats (Galef Jr., Mason, Preti, & Bean, 1988).

Acoustic stimuli with social value can also be rewarding, and several studies in male birds showed that conspecific song acts as a reinforcer. In chaffinches (*Fringilla coelebs*; Stevenson, 1967; Stevenson-Hinde, 1972), zebra finches (*Taeniopygia guttata*; Adret, 1993; Ten Cate, 1991), or domesticated canaries (*Serinus canaria*; Calhoun, Hulse, Braaten, Page, & Nelson, 1993), behavior-contingent exposure to conspecific song can be used as the sole reinforcer in operant tasks: birds visit a perch or peck a key more frequently when the action gives exposure to song.

The rewarding value of songs in operant paradigms has also been used to examine females' preference for particular song variants. On one hand, studies demonstrate the early acquired rewarding value of a given song variant for an individual female. Female zebra finches prefer to hear father's song (Riebel, Smallegange, Terpstra, & Bolhuis, 2002) or tutor song (Riebel, 2000; Riebel, Naguib, & Gil, 2009), which are heard by birds early in life, before nutritional independence (around Day 35; Zann, 1996). In this species, female song preference as adults may also depend on early developmental conditions (Holveck & Riebel, 2010; Riebel et al., 2009; Woodgate et al., 2011). On the other hand, the universal reinforcing value of particular song characteristics for females of a given species has received support from several studies: female zebra finches prefer conspecific song over heterospecific song (isolation-reared females; Braaten & Reynolds, 1999), song repertoire over single-phrase song (Collins, 1999), and songs with longer duration and containing more syllables over simpler songs (Spencer et al., 2005; Woodgate et al., 2011). Similar results have been found in female European starlings (*Sturnus vulgaris*; Gentner & Hulse, 2000) and in chaffinches (Riebel & Slater, 1998).

Alexandra M. Hernandez, Emilie C. Perez, Hervé Mulard, Nicolas Mathevon, and Clémentine Vignal, Université de Lyon/Saint-Etienne, Neuro-PSI/ENES - CNRS UMR 9197.

This work was supported by ANR grants (French Agence Nationale de la Recherche, projects 'Bird voices' and 'Acoustic Partnership') and an IUF grant to CV (Institut Universitaire de France). We are grateful to Colette Bouchut, Nicolas Boyer, Julie Elie, Ludovic Favre, and Lise Pelletier for their help during the project.

Correspondence concerning this article should be addressed to Clémentine Vignal, Université de Lyon/Saint-Etienne, Neuro-PSI/ENES - CNRS UMR 9197, 23 rue Paul Michelon, 42023 Saint-Etienne, France. E-mail: clementine.vignal@univ-st-etienne.fr

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Here we ask if an acoustic signal simpler and shorter than song can acquire a rewarding value for a female songbird during adulthood. Several studies have suggested that female preferences may be tuned by adult experience (e.g., in white-crowned sparrows, *Zonotrichia leucophrys* [MacDougall-Shackleton, MacDougall-Shackleton, & Hahn, 2001] and domesticated canaries [Depraz, Kreutzer, & Leboucher, 2004; Nagle & Kreutzer, 1997]), but none to our knowledge has demonstrated that a sound can become a reinforcing agent because of its particular social value acquired during adulthood. In this study, we investigate the potential existence of the late-acquired reinforcing value of mate's calls in female zebra finches.

Zebra finches form lifelong pair bonds and pair bonding may occur as soon as birds are sexually mature, between 2 and 3 months of age (Zann, 1996). Partners are together year-round, and synchronize their activities, perch in contact and preen one another exclusively (Zann, 1996). The central social relationship of an adult zebra finch is the one with its mate (McCowan, Mariette, & Griffith, 2015). Females are able to recognize their mate using song (Miller, 1979; Woolley & Doupe, 2008), and males as well as females show preferential vocal response to the playback of their mate's distance calls (Vignal, Mathevon, & Mottin, 2004, 2008). Distance calls are very brief (around 200 ms in males and 300 ms in females) and highly individually stereotypic vocal signals (Forstmeier, Burger, Temnow, & Derégnaucourt, 2009), uttered mainly when birds lose visual contact with their partner (Zann, 1996). In nature, separation between mates is likely to occur during bouts of foraging. Individual recognition and preferential response to mate's calls may be particularly important given the gregarious nature of this colonial nesting species and thus serves an important function in the life history of wild zebra finches.

Here we tested if female zebra finches display a preferential response toward their mate's calls, using an operant choice apparatus that allowed females to hop on a perch to hear their mate's call, and hop on another perch to hear another familiar male's call. We hypothesize that mate's call may acquire reinforcing properties to females in adulthood, and predict females will visit more frequently the perch associated with the playback of the mate's than nonmate's call.

Method

Subjects

Female zebra finches (*Taeniopygia guttata*; $N = 18$) were used in this experiment. Before experimentation females were housed in male-female breeding pairs in standard cages (40 cm H × 38 cm W × 24 cm D). All birds were maintained on 14L:10D light cycle, at 22–24 °C, with finch seed mix, cuttlefish bones, and water available ad libitum. Birds were supplemented once a week with fresh salad. All pairs had either previously raised young, or demonstrated allopreening, built nests, and incubated eggs. As such, all females used were from well bonded breeding pairs (Zann, 1996). Experiments were performed under the authorization no. 42–218-0901-38SV09 (ENES lab, DDSV Loire, France).

Apparatus

The operant choice apparatus had a larger central region and two side arms (see Figure 1). Each side arm contained a perch that was equipped with infrared sensors to monitor when the bird hopped into the arm. Beside each arm was a speaker (Bravo AudioPro Allroom Speakers, AudioPro, Sweden), connected to a computer and an amplifier setup, used for call playback and event monitoring. A hop onto either perch broke an infrared beam, triggering the playback of one call randomly selected from a pool of 10 call exemplars available for each male. After a call playback, the infrared beam needed to contact again before it could be broken to trigger a new call playback.

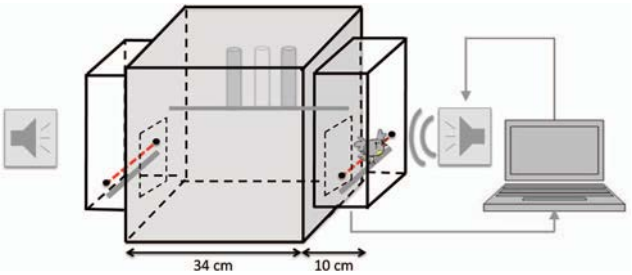


Figure 1. Schematic of the operant choice apparatus (test cage). The central region had small openings leading to side arms. Each side arm contained a perch that was equipped with infrared sensors to monitor when the bird hopped into the arm. A hop onto either perch broke an infrared beam, triggering the playback of one call randomly selected from a pool of 10 call exemplars available for each side. After a call playback, the infrared beam needed to contact again before it could be broken to trigger a new call playback. Food (gray) and water cups (white) were placed above the perch of the central region. See the online article for the color version of this figure.

The central region of the operant choice apparatus was equipped with only one perch to enhance exploration into side arms. To further encourage females to hop into the arms so that they could learn the contingency, opaque barriers were placed on the two side-walls of the central area, such that the view into the arms, and toward the playback speakers, was blocked when perched in the central area. During the test, food and water cups were placed in the center of the cage, so as not to induce a side preference, but during the three first hours of acclimatization to the experimental cage, one food cup was placed in each arm so as to encourage the bird to explore both arms. Furthermore, before placing a new bird in the apparatus, papers below the cage were changed and arms cleaned, to remove food and fecal evidence of previous bird's activity within the apparatus.

Operant Choice Protocol

Female's response to their mate's versus a familiar nonmate's distance calls (see below for a description of call stimuli) was examined in the operant choice apparatus. Females were separated from their mate and learned to hop into one arm (GO response) of the test cage to hear their mate's call or another arm of the cage to hear a familiar male's calls. After this 3-day testing session, females were all returned to their home cage with their mate. To test for stability of females' response (retention protocol; Table 1), eight females were returned to the operant apparatus for a new testing session of 3 days after 2 weeks of retention spent in their home cage with their mate. Here females' GO responses to their mate's versus the same familiar nonmate's distance calls as in the

Table 1
Details of Sample Sizes and Protocol Design

Reversal protocol ($N = 9$)		Nonreversal protocol ($N = 9$)	
One test ($N = 5$)	Two tests: Retention ($N = 4$)	One test ($N = 5$)	Two tests: Retention ($N = 4$)

first session were reassessed, and compared with original response levels.

During tests, females were placed alone in individual choice test cages within a sound attenuation chamber (Silence Box model, Tiptop Wood, Saint-Etienne, France). Females' exposure to their mate's distance calls was contingent on entering a side arm, via a small opening in the side of the central cage. Exposure to another familiar male's calls was contingent on the female entering an arm on the opposite side. Females learned they could hop to one arm to hear their mate's calls, and another arm to hear another familiar male's calls. Which arm (i.e., left or right) each female heard their mate's versus the nonmate's call was counterbalanced among birds. Furthermore for half of the birds ($N = 9$), the arm from which mate's calls versus nonmate's calls could be heard remained constant throughout the experiment (nonreversal birds; Table 1). For the others ($N = 9$) the arms were switched midway during the test (after 1.5 day) to reduce the possibility of side preferences (reversal birds; Table 1). For the females used in the retention protocol, the arm associated with mate's versus nonmate's call during the first and the second testing sessions was assigned as follows: for nonreversal birds ($N = 4$; Table 1), the sides remained the same for the two testing sessions; for reversal birds ($N = 4$; Table 1), if the first testing session started with mate's calls on the left side, it changed after 1.5 day of test to mate's calls on the right side, and the second testing session then started with mate's calls on the right side and after 1.5 day of test it changed to mate's calls on the left side.

Call Stimuli

Recordings of all male distance calls were made from a distance of approximately 30 cm using a Sennheiser MD42 microphone connected to a Marantz PMD680 digital recorder at 44.1 kHz. Ten distance call exemplars per bird, randomly selected from a group of high quality recordings, were used in this experiment. Sound files were high pass filtered above 250 Hz and then amplitude was normalized among all recordings and maximized using GoldWave Software (Version 5.22, 2007, GoldWave Inc., St. John's, Canada).

Recordings used as familiar nonmate playback stimuli were selected from among the males from the other breeding pairs housed in the same breeding room before experimentation. Female subjects and males whose calls were used as familiar nonmate stimuli were considered familiar as their cages allowed both visual and acoustic contact and they were housed in the same room for at least 4 weeks before the experiments. As such, all nonmate recordings were of familiar males and of males in breeding pairs. Which male served as nonmate stimuli for each female was selected in a manner to best match the length of their mate's distance call. This reduced the possible influence of call length (Vicario, Naqvi, & Raksin, 2011) on female responses. Once selected, the same nonmate stimuli were used across the experiment for a given female.

Data Analysis and Statistics

The tests were each three days in duration. The number of events in the mate versus nonmate arms was determined during the entire test. Only daytime events were considered, as bird are not active during the night. All statistical tests were performed using R software (R Development Core Team, 2007, version 3.0.2). All results in the text and in tables are presented with 95% confidence intervals. Before *t* tests, normality of the data was tested using Shapiro-Wilk test and homogeneity of variances was checked using *F* test. Effect sizes of *t* tests were assessed using Cohen's *d*.

All models were checked for normality and homogeneity by visual inspections of plots of residuals (plotresid function, RVAideMemoire library). *p* values were obtained on models using Wald χ^2 tests (analysis of variance [ANOVA] function, car library). Effect sizes are presented as marginal and conditional coefficients of determination (r2m and r2c, r.squaredGLMM function of the MuMIn package) as well as estimates, *SE*s, and 95% confidence intervals of fixed factors.

Female preference was tested using the total number of hops in mate versus nonmate arms using data of the first test of all females ($N = 18$; Table 1). The total number of hops was log-transformed and tested using a linear mixed model (LMM, lmer function of the lme4 package) with the stimulus (two levels: mate, nonmate) as fixed factor and the female identity (18 levels) nested in the protocol (two levels: Reversal, Nonreversal) as random factors. The relative mate call preference, that is, the ratio of the number of events in mate arm divided by the total number of events in mate and nonmate arms, was also compared with 0.5 with a *t* test. The absence of preference between mate and nonmate call would translate to a ratio not different from 0.5, and a preference for nonmate over mate in a ratio significantly lower than 0.5.

The effect of the reversal protocol on the total number of hops (log-transformed) and the relative mate call preference was tested using *t* tests on data of the first test of all females ($N = 18$; Table 1). To test for the stability of the response of females after 2 weeks of retention, the total number of hops was log-transformed and tested using a LMM with the stimulus (two levels: mate, nonmate) and the session (two levels: first, second) as fixed factors and the female identity (eight levels) nested in the protocol (two levels: Reversal, Nonreversal) as random factors. There was no effect of the interaction of the two fixed factors. The relative mate call preference was tested using a LMM with the session (two levels: first, second) as fixed factor and the female identity (eight levels) nested in the protocol (two levels: Reversal, Nonreversal) as random factors.

Results

Female Preference for Mate's Calls

As hypothesized, females produced significantly more hops to hear their mate's call (mate) than the calls of another familiar male (nonmate; Figure 2, Table 2; $\chi^2_1 = 13.15$, $p = .0003$, r2m = 0.06, r2c = 0.85). Despite variability between females in number of

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

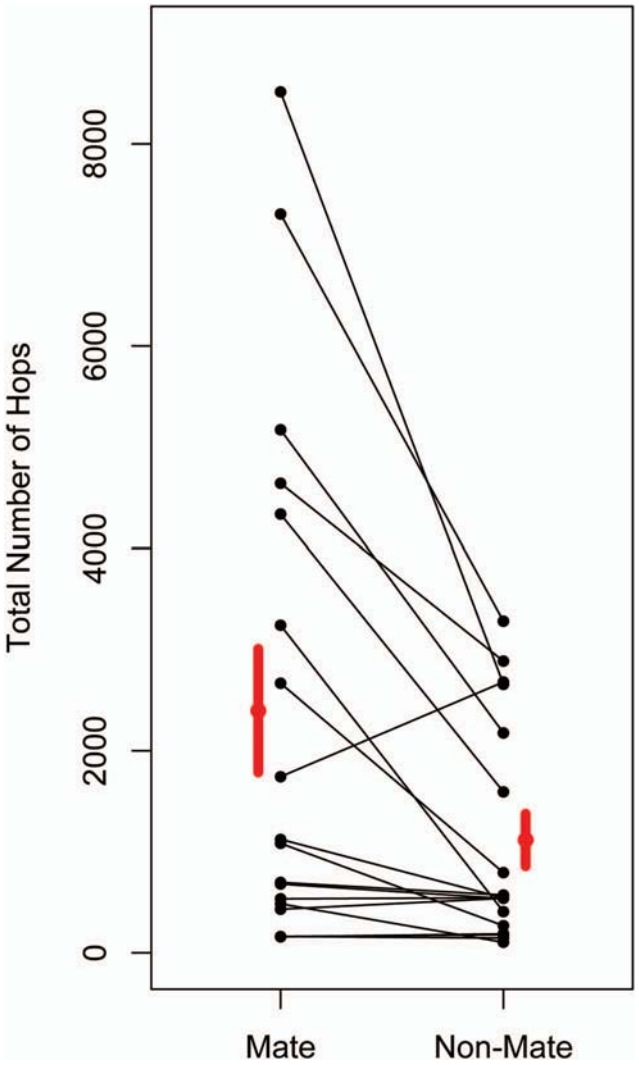


Figure 2. Total number of hopping events to hear mate's versus nonmate's distance calls. Points with bars are mean ± *SE* values on all individuals ($N = 18$). Lines connect paired values from same individuals. See the online article for the color version of this figure.

hops, 13 of the 18 females produced more hops to hear their mate's call than the calls of another familiar male (see Figure 2). The relative mate call preference, that is, the ratio of the number of events in mate arm divided by the total number of events in mate and nonmate arms, confirms this result as it was significantly higher than 0.5 (mean [95% CI]: 0.63 [0.55–0.70], $t = 3.58$, $df = 17$, $p = .0023$, $d = 0.84$).

Table 2
Effect of Stimulus Identity on Females' Number of Hops in the Operant Choice Cage

Stimulus	Raw mean	Estimate	*SE*	Lower CI	Upper CI
Mate	2,397	3.079	.168	1.35	4.8
Nonmate	1,117	2.818	.168	1.09	4.54

Note. Estimates, *SE*s, lower confidence interval (CI), and upper CI are results of the LMM on $\log_{10}$ (number of hops).

Effects of Reversal Protocol on Operant Behavior

Despite a tendency in reversal birds to hop less during the test, reversal and nonreversal birds did not differ significantly in total number of hops (mean reversal: 2520.3, nonreversal: 4494.8; mean $\log_{10}$ [95% CI] reversal: 3.09 [2.74–3.45] versus nonreversal: 3.48 [3.18–3.77], $t = -1.65$, $df = 15.35$, $p = .1185$, $d = 0.74$).

Birds in the protocol with reversal showed lower relative mate call preference than birds in the protocol without side reversal (Figure 3, mean [95% CI] reversal: 0.53 [0.45–0.61], nonreversal: 0.73 [0.66–0.80], $t = -3.71$, $df = 15.46$, $p = .0020$, $d = 1.32$).

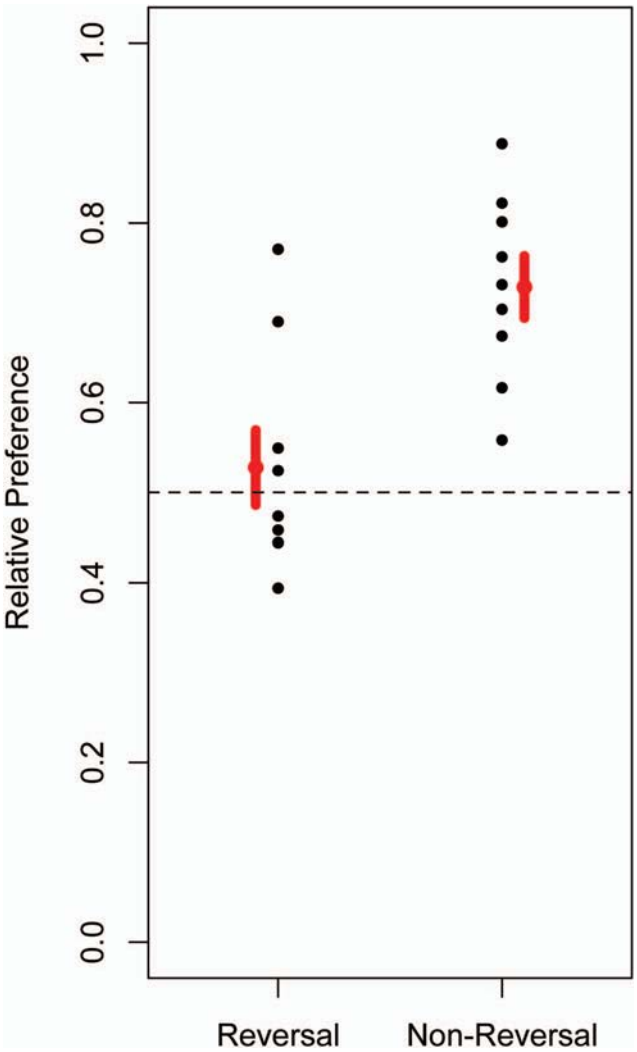


Figure 3. Impact of side reversal protocol on relative mate's call preference (ratio of the number of events in mate arm on the total number of events in mate and nonmate arms). Points with bars are mean ± *SE* values on all individuals ($N = 18$). Black points are individual values. See the online article for the color version of this figure.

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Stability of Female Preference for Mate's Calls

After 2 weeks of retention back with their mate in their home cage, females still produced more hops to hear their mate's call than the calls of another familiar male (Table 3; $\chi^2_1 = 7.30$, $p = .0069$, r2m = 0.17, r2c = 0.69), but females did fewer hops during the second session than during the first (Table 3; $\chi^2_1 = 9.97$, $p = .0016$). First and second session did not differ statistically in relative mate call preference (Figure 4, Table 4; $\chi^2_1 = 0.515$, $p = .473$, r2m = 0.02, r2c = 0.30), but 6 out of 8 females increased their relative mate call preference between sessions.

Discussion

Here we show that mates' calls are rewarding to female zebra finches, as they visited more frequently the perch associated with the playback of mate's call in the operant task. Because all birds were experimentally paired in the laboratory, a preference for a particular call variant preceding pairing can be excluded, so we demonstrated here the late-acquired reinforcing value of mate's calls in a monogamous female songbird.

Because mated males were used as the call source for mate calls and familiar calls, females' responses can be attributed to call identity rather than a preference for a signal of pairing status in calls of mated males. By pitting mate's call against a familiar male's call, as opposed to an unfamiliar male's call, we can interpret females' responses in the present study to be based on discrimination of mate's call and not simply a preference for familiarity (see O'Loghlen & Beecher, 1999, for further discussion of this issue). Before the tests, females were housed with their mate in breeding cages, so females had acoustic, visual, and physical contact with their mate, whereas with familiar males, housed with their own female partners, they only had acoustic and visual contact. In zebra finches, acoustic and visual contact is sufficient to allow social interaction (Zann, 1996), but the level and intensity of social interactions of the females were obviously not the same with their mate and with the familiar male. This is similar to what would happen in a social group, as adult zebra finches have physical interactions (perching in contact and preening one another) almost exclusively with their mate (Zann, 1996) and the central social relationship of an adult zebra finch is its mate (McCowan et al., 2015). While the possibility that mate calls were simply more familiar to the female subject than the calls of the neighboring familiar male in our experiment cannot be totally excluded, this could not be ruled out by testing females living in a social group as females would still interact mostly or exclusively with their mate. To investigate the impact of the level of familiarity without the confounding effect of the pair-bond relationship, level of familiarity could be artificially controlled by exposing females to the playback of male calls during housing or by designing housing cages that allow comparable levels of familiarity of the female with the mate and the nonmate males.

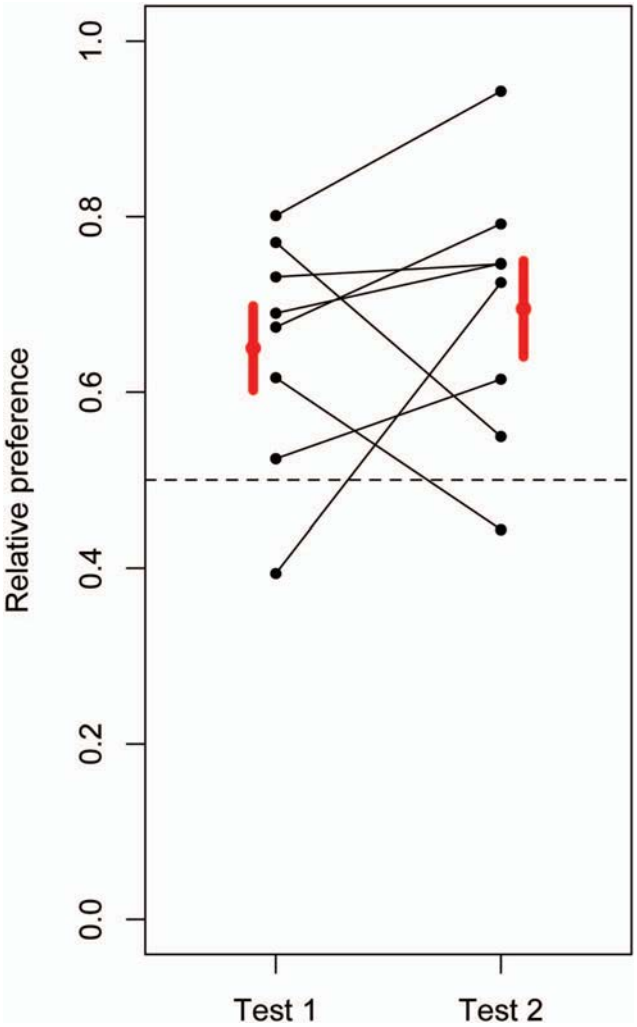


Figure 4. Stability of relative mate's call preference between first and second tests. Points with bars are mean ± *SE* values on all individuals ($N = 8$). Lines connect paired values from same individuals. See the online article for the color version of this figure.

Table 3
Effect of Stimulus Identity and Test Number (Retention) on Females' Number of Hops in the Operant Choice Cage

Factor	Raw mean	Estimate	*SE*	Lower CI	Upper CI
Mate	2,344	3.093	.194	2.65	3.53
Nonmate	1,194	2.741	.194	2.3	3.18
Test 1	2,204	3.123	.194	2.68	3.56
Test 2	1,335	2.711	.194	2.27	3.15

Note. Estimates, *SE*s, lower confidence interval (CI), and upper CI are results of the LMM on $\log_{10}$ (number of hops). The interaction between stimulus identity and test number was not significant.

Table 4
Effect of Test Number (Retention) on Females' Relative Preference for Mate Calls Over Nonmate Calls in the Operant Choice Cage

Test	Raw mean	Estimate	*SE*	Lower CI	Upper CI
Test 1	.65	.6503	.0554	.42	.88
Test 2	.695	.695	.0554	.465	.925

Note. Estimates, *SE*s, lower confidence interval (CI), and upper CI are results of the LMM on the relative preference.

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Our results confirm that female zebra finches are able to recognize their mate's using distance calls alone (Vignal et al., 2004, 2008). In addition, these findings suggest that hearing mate's calls is more reinforcing than hearing a familiar nonmate's calls. In previous studies, female zebra finches have shown stronger operant responses to their own species song when pitted against another species (Braaten & Reynolds, 1999), and to father's (Riebel et al., 2002) or tutor's (Riebel, 2000) song when pitted against an unfamiliar males song. However, calls are generally much shorter in duration and less complex in acoustic structure than songs. They are also less linked to the courtship context, and one can hypothesize that they could be less rewarding than songs. The present study shows that calls can also be reinforcing to female zebra finches, and more specifically that the mate's distance call is more reinforcing than another familiar male's call.

In the present study, we measured using an operant choice apparatus the preference of females to hear their mate's calls over another familiar male's calls. We do not know if the preference to hear mates' calls expressed by females relates to a mate choice decision. Whether females would express the same preference direction if given the choice to pair between the two males producing the calls used as stimuli remains to be studied but is likely. Indeed, a previous study showed that female zebra finches' mating preferences are consistent across three different testing contexts: an operant test with songs, a phonotaxis test with songs and an association test with live males (Holveck & Riebel, 2007).

Female songbirds' auditory preference is known to be tuned by adult experience (e.g., Depraz et al., 2004; MacDougall-Shackleton et al., 2001; Nagle & Kreutzer, 1997). By showing that mate's calls are rewarding to females, our results suggest that signals with social value acquired during adulthood, can act as reinforcing agents. This reinforcing value of mate's calls could be involved in the maintenance of the monogamous pair-bond of the zebra finch. Indeed, bonded partners show mutual calling in several situations: time-locked soft calls exchanges occur between mates both when separately housed or when housed in a social group (Ter Maat, Trost, Sagunsky, Seltmann, & Gahr, 2014). Mates exchange calls when physically separated and adapt their calling dynamics depending on visual cues (Perez, Fernandez, Griffith, Vignal, & Soula, 2015). Partners use coordinated calls exchanges at the nest during breeding that can be described as call duets (Elie et al., 2010). Future studies should further explore the role of the brain reward system on auditory preferences and pair-bond maintenance. The mesolimbic reward system has been shown to be involved in pair-bond formation and maintenance as well as in partner's preference in voles, and the pair-bond has been proposed to be a conditioned partner preference strengthened by mating (Young & Wang, 2004). In zebra finches, the activation of immediate-early genes in the nucleus taeniae, a neural structure akin to the amygdala, correlates with female's mate-directed behaviors, like clumping and preening (Svec, Licht, & Wade, 2009), suggesting an implication of the mesolimbic system in mate preference. Several recent studies showed the involvement of the neuropeptides mesotocin and vasotocin (the avian homolog of oxytocin and vasopressin; Kelly & Goodson, 2014; Pedersen & Tomaszycki, 2012) and of the vasoactive intestinal polypeptide (VIP; Kingsbury & Goodson, 2014) in pair-bonding regulation in zebra finches. Whether these peptides can participate in shaping auditory preferences, to our knowledge, remains to be investigated.

As a last point, we want to stress that our study is preliminary because of relatively low sample size and shows some limitations. We observed that the side reversal protocol had an impact on the females' mate call preference in the operant task (lower relative mate call preference), but also on the motivation of the birds to perform the task (tendency to hop less). Side reversal protocols have been classically used to control for potential side bias during operant task in birds (e.g., Holveck & Riebel, 2007; Riebel & Slater, 1998; Riebel et al., 2002). It is possible that after reversal, the females needed some time to relearn the location of the stimuli and failed to show mate call preference during the first hours. Another possibility is that the side reversal protocol compromised learning of the task. To test these hypotheses, a comparison is needed between the performances of the females tested with or without reversal protocol both before and after switching the sides of the stimuli. As our test was relatively short (3 days), increasing the time spent by the bird in the set-up could perhaps improve females' mate call preference by giving more time to relearn the sides, but it could also decrease the motivation of the bird to perform the task. Indeed, we also showed that, during a second session of test, females still preferred to hear their mate's calls but were less active (hopped less).

In this study we showed using an operant choice apparatus that mate's calls, which are acoustic signals significantly simpler and shorter than song, are rewarding for female zebra finches. Whether the rewarding property of mate's calls may promote learning in the context of pair-bonding, supporting the maintenance of the pair-bond, remains to be investigated.

References

Adret, P. (1993). Operant conditioning, song learning and imprinting to taped song in the zebra finch. *Animal Behaviour, 46,* 149–159. http://dx.doi.org/10.1006/anbe.1993.1170

Al-Imari, L., & Gerlai, R. (2008). Sight of conspecifics as reward in associative learning in zebrafish (*Danio rerio*). *Behavioural Brain Research, 189,* 216–219. http://dx.doi.org/10.1016/j.bbr.2007.12.007

Blatter, K., & Schultz, W. (2006). Rewarding properties of visual stimuli. *Experimental Brain Research, 168,* 541–546. http://dx.doi.org/10.1007/s00221-005-0114-y

Braaten, R. F., & Reynolds, K. (1999). Auditory preference for conspecific song in isolation-reared zebra finches. *Animal Behaviour, 58,* 105–111. http://dx.doi.org/10.1006/anbe.1999.1134

Brannon, E. M., Andrews, M. W., & Rosenblum, L. A. (2004). Effectiveness of video of conspecifics as a reward for socially housed bonnet macaques (*Macaca radiata*). *Perceptual and Motor Skills, 98,* 849–858. http://dx.doi.org/10.2466/pms.98.3.849-858

Calhoun, S., Hulse, S. H., Braaten, R. F., Page, S. C., & Nelson, R. J. (1993). Responsiveness to conspecific and alien song by canaries (*Serinus canaria*) and European starlings (*Sturnus vulgaris*) as a function of photoperiod. *Journal of Comparative Psychology, 107,* 235–241. http://dx.doi.org/10.1037/0735-7036.107.3.235

Collins, S. A. (1999). Is female preference for male repertoires due to sensory bias? *Proceedings of the Royal Society of London, Series B: Biological Sciences, 266,* 2309–2314. http://dx.doi.org/10.1098/rspb.1999.0924

Coureaud, G., Moncomble, A.-S., Montigny, D., Dewas, M., Perrier, G., & Schaal, B. (2006). A pheromone that rapidly promotes learning in the newborn. *Current Biology, 16,* 1956–1961. http://dx.doi.org/10.1016/j.cub.2006.08.030

Deaner, R. O., Khera, A. V., & Platt, M. L. (2005). Monkeys pay per view: Adaptive valuation of social images by rhesus macaques. *Current Biology, 15,* 543–548. http://dx.doi.org/10.1016/j.cub.2005.01.044

Depraz, V., Kreutzer, M., & Leboucher, G. (2004). Sexual preferences for songs in female domestic canaries (*Serinus canaria*): Can late song exposure, without social reinforcement, influence the effects of early tutoring? *Acta Ethologica, 6,* 73–78. http://dx.doi.org/10.1007/s10211-004-0088-y

Douglas, L. A., Varlinskaya, E. I., & Spear, L. P. (2004). Rewarding properties of social interactions in adolescent and adult male and female rats: Impact of social versus isolate housing of subjects and partners. *Developmental Psychobiology, 45,* 153–162. http://dx.doi.org/10.1002/dev.20025

Elie, J. E., Mariette, M. M., Soula, H. A., Griffith, S. C., Mathevon, N., & Vignal, C. (2010). Vocal communication at the nest between mates in wild zebra finches: A private vocal duet? *Animal Behaviour, 80,* 597–605. http://dx.doi.org/10.1016/j.anbehav.2010.06.003

Forstmeier, W., Burger, C., Temnow, K., & Derégnaucourt, S. (2009). The genetic basis of zebra finch vocalizations. *Evolution; International Journal of Organic Evolution, 63,* 2114–2130. http://dx.doi.org/10.1111/j.1558-5646.2009.00688.x

Galef, B. G., Jr., Mason, J. R., Preti, G., & Bean, N. J. (1988). Carbon disulfide: A semiochemical mediating socially-induced diet choice in rats. *Physiology & Behavior, 42,* 119–124. http://dx.doi.org/10.1016/0031-9384(88)90285-5

Gentner, T. Q., & Hulse, S. H. (2000). Female European starling preference and choice for variation in conspecific male song. *Animal Behaviour, 59,* 443–458. http://dx.doi.org/10.1006/anbe.1999.1313

Gerlai, R., & Hogan, J. A. (1992). Learning to find the opponent: An ethological analysis of the behavior of paradise fish (*Macropodus opercularis*) in intra- and interspecific encounters. *Journal of Comparative Psychology, 106,* 306–315. http://dx.doi.org/10.1037/0735-7036.106.3.306

Gil, M., Nguyen, N.-T., McDonald, M., & Albers, H. E. (2013). Social reward: Interactions with social status, social communication, aggression, and associated neural activation in the ventral tegmental area. *European Journal of Neuroscience, 38,* 2308–2318. http://dx.doi.org/10.1111/ejn.12216

Holveck, M.-J., & Riebel, K. (2007). Preferred songs predict preferred males: Consistency and repeatability of zebra finch females across three test contexts. *Animal Behaviour, 74,* 297–309. http://dx.doi.org/10.1016/j.anbehav.2006.08.016

Holveck, M.-J., & Riebel, K. (2010). Low-quality females prefer low-quality males when choosing a mate. *Proceedings of the Royal Society B: Biological Sciences, 277,* 153–160. http://dx.doi.org/10.1098/rspb.2009.1222

Humphreys, A. P., & Einon, D. F. (1981). Play as a reinforcer for maze-learning in juvenile rats. *Animal Behaviour, 29,* 259–270. http://dx.doi.org/10.1016/S0003-3472(81)80173-X

Ikemoto, S., & Panksepp, J. (1992). The effects of early social isolation on the motivation for social play in juvenile rats. *Developmental Psychobiology, 25,* 261–274. http://dx.doi.org/10.1002/dev.420250404

Kelly, A. M., & Goodson, J. L. (2014). Hypothalamic oxytocin and vasopressin neurons exert sex-specific effects on pair bonding, gregariousness, and aggression in finches. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 111,* 6069–6074. http://dx.doi.org/10.1073/pnas.1322554111

Kingsbury, M. A., & Goodson, J. L. (2014). Pair bond formation is impaired by VPAC receptor antagonism in the socially monogamous zebra finch. *Behavioural Brain Research, 272,* 264–268. http://dx.doi.org/10.1016/j.bbr.2014.06.042

Lee, A., Clancy, S., & Fleming, A. S. (1999). Mother rats bar-press for pups: Effects of lesions of the mpoa and limbic sites on maternal behavior and operant responding for pup-reinforcement. *Behavioural Brain Research, 100,* 15–31. http://dx.doi.org/10.1016/S0166-4328(98)00109-0

MacDougall-Shackleton, S. A., MacDougall-Shackleton, E. A., & Hahn, T. P. (2001). Physiological and behavioural responses of female mountain white-crowned sparrows to natal- and foreign-dialect songs. *Canadian Journal of Zoology, 79,* 325–333. http://dx.doi.org/10.1139/z00-207

McCowan, L. S. C., Mariette, M. M., & Griffith, S. C. (2015). The size and composition of social groups in the wild zebra finch. *Emu, 115,* 191–198. http://dx.doi.org/10.1071/MU14059

Miller, D. B. (1979). The acoustic basis of mate recognition by female Zebra finches (*Taeniopygia guttata*). *Animal Behaviour, 27,* 376–380. http://dx.doi.org/10.1016/0003-3472(79)90172-6

Nagle, L., & Kreutzer, M. L. (1997). Adult female domesticated canaries can modify their song preferences. *Canadian Journal of Zoology, 75,* 1346–1350. http://dx.doi.org/10.1139/z97-759

Normansell, L., & Panksepp, J. (1990). Effects of morphine and naloxone on play-rewarded spatial discrimination in juvenile rats. *Developmental Psychobiology, 23,* 75–83. http://dx.doi.org/10.1002/dev.420230108

O'Loghlen, A. L., & Beecher, M. D. (1999). Mate, neighbour and stranger songs: A female song sparrow perspective. *Animal Behaviour, 58,* 13–20. http://dx.doi.org/10.1006/anbe.1999.1125

Pedersen, A., & Tomaszycki, M. L. (2012). Oxytocin antagonist treatments alter the formation of pair relationships in zebra finches of both sexes. *Hormones and Behavior, 62,* 113–119. http://dx.doi.org/10.1016/j.yhbeh.2012.05.009

Perez, E. C., Fernandez, M. S., Griffith, S. C., Vignal, C., & Soula, H. A. (2015). Impact of visual contact on vocal interaction dynamics of pair-bonded birds. *Animal Behaviour, 107,* 125–137. http://dx.doi.org/10.1016/j.anbehav.2015.05.019

R Development Core Team. (2007). R: A language and environment for statistical computing (Version 3.0.2) [Computer Software]. Vienna, Austria: Author. Retrieved from https://www.R-project.org

Riebel, K. (2000). Early exposure leads to repeatable preferences for male song in female zebra finches. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 267,* 2553–2558. http://dx.doi.org/10.1098/rspb.2000.1320

Riebel, K., Naguib, M., & Gil, D. (2009). Experimental manipulation of the rearing environment influences adult female zebra finch song preferences. *Animal Behaviour, 78,* 1397–1404. http://dx.doi.org/10.1016/j.anbehav.2009.09.011

Riebel, K., & Slater, P. J. B. (1998). Testing female chaffinch song preferences by operant conditioning. *Animal Behaviour, 56,* 1443–1453. http://dx.doi.org/10.1006/anbe.1998.0933

Riebel, K., Smallegange, I. M., Terpstra, N. J., & Bolhuis, J. J. (2002). Sexual equality in zebra finch song preference: Evidence for a dissociation between song recognition and production learning. *Proceedings Biological Sciences, 269,* 729–733. http://dx.doi.org/10.1098/rspb.2001.1930

Rnic, A. (1977). Male versus female Siamese fighting fish as reinforcing stimuli for conspecific males in single- and two-choice operant situations. *Learning and Motivation, 8,* 263–274. http://dx.doi.org/10.1016/0023-9690(77)90010-8

Spencer, K. A., Wimpenny, J. H., Buchanan, K. L., Lovell, P. G., Goldsmith, A. R., & Catchpole, C. K. (2005). Developmental stress affects the attractiveness of male song and female choice in the zebra finch (*Taeniopygia guttata*). *Behavioral Ecology and Sociobiology, 58,* 423–428. http://dx.doi.org/10.1007/s00265-005-0927-5

Stevenson, J. G. (1967). Reinforcing effects of chaffinch song. *Animal Behaviour, 15,* 427–432. http://dx.doi.org/10.1016/0003-3472(67)90040-1

Stevenson-Hinde, J. (1972). Effects of early experience and testosterone on song as a reinforcer. *Animal Behaviour, 20,* 430–435. http://dx.doi.org/10.1016/S0003-3472(72)80004-6

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Svec, L. A., Licht, K. M., & Wade, J. (2009). Pair bonding in the female zebra finch: A potential role for the nucleus taeniae. *Neuroscience, 160,* 275–283. http://dx.doi.org/10.1016/j.neuroscience.2009.02.003

Taylor, G. T. (1981). Fear and affiliation in domesticated male rats. *Journal of Comparative and Physiological Psychology, 95,* 685–693. http://dx.doi.org/10.1037/h0077817

Ten Cate, C. (1991). Behaviour-contingent exposure to taped song and zebra finch song learning. *Animal Behaviour, 42,* 857–859. http://dx.doi.org/10.1016/S0003-3472(05)80131-9

Ter Maat, A., Trost, L., Sagunsky, H., Seltmann, S., & Gahr, M. (2014). Zebra finch mates use their forebrain song system in unlearned call communication. *PLoS ONE, 9,* e109334. http://dx.doi.org/10.1371/journal.pone.0109334

Thompson, T. I. (1963). Visual Reinforcement in Siamese Fighting Fish. *Science, 141,* 55–57. http://dx.doi.org/10.1126/science.141.3575.55

Thompson, T. I. (1964). Visual reinforcement in fighting cocks. *Journal of the Experimental Analysis of Behavior, 7,* 45–49. http://dx.doi.org/10.1901/jeab.1964.7-45

Trezza, V., Campolongo, P., & Vanderschuren, L. J. M. J. (2011). Evaluating the rewarding nature of social interactions in laboratory animals. *Developmental Cognitive Neuroscience, 1,* 444–458. http://dx.doi.org/10.1016/j.dcn.2011.05.007

Tzschentke, T. M. (2007). Measuring reward with the conditioned place preference (CPP) paradigm: Update of the last decade. *Addiction Biology, 12,* 227–462. http://dx.doi.org/10.1111/j.1369-1600.2007.00070.x

Vicario, D. S., Naqvi, N. H., & Raksin, J. N. (2001). Sex differences in discrimination of vocal communication signals in a songbird. *Animal Behaviour, 61,* 805–817. http://dx.doi.org/10.1006/anbe.2000.1651

Vignal, C., Mathevon, N., & Mottin, S. (2004). Audience drives male songbird response to partner's voice. *Nature, 430,* 448–451. http://dx.doi.org/10.1038/nature02645

Vignal, C., Mathevon, N., & Mottin, S. (2008). Mate recognition by female zebra finch: Analysis of individuality in male call and first investigations on female decoding process. *Behavioural Processes, 77,* 191–198. http://dx.doi.org/10.1016/j.beproc.2007.09.003

Woodgate, J. L., Leitner, S., Catchpole, C. K., Berg, M. L., Bennett, A. T. D., & Buchanan, K. L. (2011). Developmental stressors that impair song learning in males do not appear to affect female preferences for song complexity in the zebra finch. *Behavioral Ecology, 22,* 566–573. http://dx.doi.org/10.1093/beheco/arr006

Woolley, S. C., & Doupe, A. J. (2008). Social context-induced song variation affects female behavior and gene expression. *PLoS Biology, 6,* e62. http://dx.doi.org/10.1371/journal.pbio.0060062

Young, L. J., & Wang, Z. (2004). The neurobiology of pair bonding. *Nature Neuroscience, 7,* 1048–1054. http://dx.doi.org/10.1038/nn1327

Zann, R. A. (1996). *The Zebra Finch: A synthesis of field and laboratory studies*. New York, NY: Oxford University Press.

Received December 7, 2014
Revision received September 28, 2015
Accepted September 29, 2015 ■

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.