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High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution

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Male–female pair bonds are common to most bird species, and these bonds affect fundamental aspects of mating systems and the strength of selection, for example, by limiting extrapair paternity. Therefore, understanding factors that strengthen and erode pair bonds are important in elucidating the selection pressures that avian populations will experience. Here, we studied the effects of environmental noise on pair bonds and the strength of pair preferences (i.e. preferences for a pair-bonded partner versus an unfamiliar individual) in the monogamous zebra finch, *Taeniopygia guttata*, a model species in studies of sexual selection. Based on a previous study, we hypothesized that high-amplitude environmental noise would decrease the strength of pair preferences. Explicitly, we tested whether females' relative preference for their pair-bonded males, compared with extrapair males, decreased as the amplitude of environmental white noise increased. Our results generally supported our hypothesis, as females' preference for their pair-bonded males significantly decreased under conditions of high environmental noise. This erosion of preference may result from the masking or distortion of the paired males' pair-bond maintaining call, although the decrease in preference could also occur because a female cannot recognize her pair-bonded male. Our findings suggest that songbird populations in areas with high environmental noise may have (temporarily or permanently) weakened pair bonds, suggesting that extrapair behaviours could increase in areas of greater environmental noise.

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Most birds are socially monogamous and form pair bonds that commonly affect patterns of parental care as well as subsequent breeding attempts (e.g. Bradley et al. 1990; Smith et al. 2000; Dearborn 2001; Hasselquist & Sherman 2001; Bried et al. 2003). Pair bonds not only affect many aspects of cooperative breeding behaviours between males and females, but also mask extensive variation in extrapair behaviours and extrapair paternity, EPP (Griffith et al. 2002; Westneat & Stewart 2003; Neudorf 2004). EPP occurs in the majority of monogamous avian species (Griffith et al. 2002) and is known to affect the strength of selection acting in populations (reviewed in: Petrie &

Kempnaers 1998; Hasselquist & Sherman 2001; Griffith et al. 2002; Westneat & Stewart 2003; Neudorf 2004). Therefore, understanding how avian pair bonds are maintained and, specifically, understanding the conditions under which pair bonds are (temporarily) weakened is fundamental to estimating the selection regimes that monogamous populations experience. Here, we propose and test a novel ecological factor that could help explain the erosion of pair bonds and pair preference in the monogamous zebra finch, *Taeniopygia guttata*. Specifically, we investigated whether increasing amplitude of environmental noise weakens pair bonds in adult zebra finches and increases extrapair preferences.

Zebra finches are renowned for their strong pair bonds and low rates of EPP in the wild, often resulting in approximately 3% extrapair offspring (Birkhead et al. 1990; Zann 1996; Remage-Healey et al. 2003). It is

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thought that, once formed, zebra finch pair bonds are seldom broken while both individuals are alive and remain in the same population (Zann 1996). Given a choice between her pair-bonded male and a novel male, a paired female zebra finch will consistently prefer her familiar, pair-bonded male over a potential extrapair male in preference tests (Clayton 1990; Zann 1996).

Zebra finch pair bonds are established and maintained through a series of visual, tactile and auditory cues and signals (Zann 1996). Vocalizations that seem important to bond maintenance include the 'distance', 'tet' and 'stack' calls (Zann 1996; Swaddle et al. 2006). Of these three, the distance call is loudest (Zann 1996). It is believed to reveal individuals' identities and allow pairs to maintain contact when visually separated (Zann 1996). Tet calls, which are much softer, are zebra finches' most frequent call (Zann 1996). Apparently, tet calls encourage a partner to stay spatially nearby (Zann 1996). Stack calls have an intermediate amplitude, and zebra finches perform these calls when they are separated from their mates (Zann 1996).

In noisy and dense captive conditions, rates of EPP in zebra finch populations can be reasonably high, ranging from 11% (Birkhead et al. 1989) to 30% (Burley et al. 1996), implying that ecological factors are important in determining within-species variation in EPP. In addition, Swaddle et al. (2006) recently noted that, in preference tests performed in the presence of moderately high-amplitude white noise (approximately 75 dB), paired females consistently prefer an extrapair male to their pair-bonded male. This amplitude of noise probably masks the soft tet and intermediate stack calls, but not the loud distance calls (Swaddle et al. 2006). Therefore, we hypothesized that high-amplitude, broad-frequency noise from the environment may mask aspects of important auditory signals that maintain pair bonds, thus weakening females' preferences for their pair-bonded males.

We tested this hypothesis experimentally by assaying females' preferences for their pair-bonded mate versus an extrapair male in dichotomous preference tests under three amplitudes of environmental white noise. In these preference tests we controlled for the degree of male visual courtship display. Swaddle et al. (2006) did not vary levels of background noise, thus precluding an explicit examination of the effects of noise levels on females' preferences, nor did they account for variation in male behaviour. Therefore, the present study reflects a significant methodological

improvement for testing whether background noise alters female zebra finches' preference for pair-bonded males. We predicted that females would prefer their pair-bonded males in the low-amplitude noise condition but this preference would weaken and, perhaps, invert in the high-amplitude noise treatment, making extrapair males relatively preferred in situations of increasing environmental noise.

METHODS

We arbitrarily paired 20 male and 20 female adult zebra finches from our large, outbred, captive colony. Birds in this colony had experienced only one generation of captive breeding since being caught from the wild. Each pair was housed in individual cages (approximately 50 × 40 × 30 cm) in full-spectrum lighting on a 14:10 h light:dark cycle at approximately 20°C, in two separate rooms. Each cage was supplied with nutritionally complete seed mix, water and cuttlebone ad libitum. We also provided nesting boxes and abundant nesting materials. All finches were paired for at least 4 months before the start of the mate preference trials, and all pairs built nests, laid eggs and attempted to raise a clutch, indicating that they had formed pair bonds (Zann 1996).

We conducted preference tests in a three-chamber apparatus (Fig. 1) located in a separate room from the breeding cages. There were no cages in the test room except for the experimental chamber. Environmental conditions in the test room were similar to those of the breeding rooms, except for environmental noise, which is described below. Each female experienced three mate preference trials, corresponding to three treatments: high-amplitude white noise (90 dB), intermediate-amplitude white noise (75 dB) and low-amplitude white noise (45 dB). The order of these treatments was randomly determined for each female. To produce the different treatments, we played a white noise CD through portable speakers placed in the central chamber and recorded decibel readings using a digital sound meter (Extech 407727 with C weighting) placed in the centre of the females' preference cage (Fig. 1). For the low-amplitude treatment, no white noise was played from the CD because the HVAC system of the animal facility produced 45 dB of ambient noise without supplementation. During trials, the air conditioning

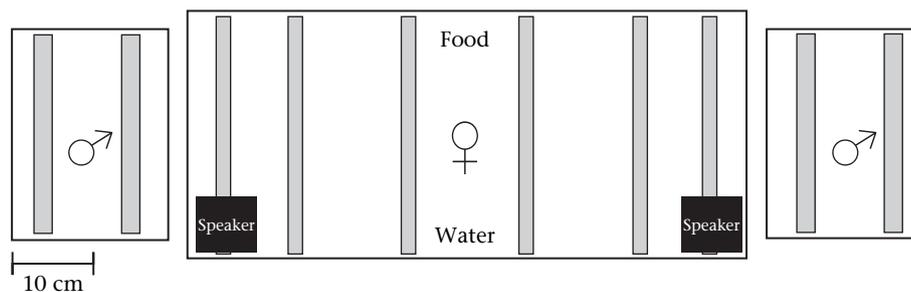


Figure 1. Plan view of the preference apparatus. The grey bars represent perches and the two boxes in the corner of the female's cage represent speakers that played white noise. The speakers were situated under the perches, approximately 10 cm from a bird on the closest perch, and thus, did not obstruct the view of any bird in the apparatus.

unit for that room was turned off so that background noise did not vary during preference tests. We chose 90 dB as the upper threshold because a previous experiment indicated that male zebra finches can modulate their display calls to approximately that amplitude (Cynx et al. 1998). Our own measurements of zebra finch vocalizations in our breeding aviary indicated that environmental noise exceeds 100 dB at times and is regularly in the 80- to 90-dB range. In addition, field measurements of environmental noise in Northern Queensland, where zebra finches breed, often exceed 120 dB, and during sustained choruses of cicadas, noise levels average 90–100 dB in zebra finch breeding habitat (J.P.S., unpublished data).

In our experimental chamber, we also recorded the noise amplitude on the display perches, which were closer to the speaker than they were to the middle of the chamber, so we could better interpret the noise that a female would experience. At 10 cm from the closest speaker (which was the approximate distance of an average displaying female), females experienced white noise at approximately 96 dB in the high-amplitude treatment, approximately 81 dB in the intermediate-noise treatment and 45 dB in the low-amplitude treatment. The maximum diameter of each speaker cone was approximately 6 cm; therefore, a distance of 10 cm is likely to be at the edge of near-field effects, making our sound meter recordings less accurate for measurements close to each speaker. However, overall, we do not think that amplitude exceeded approximately 100 dB for even the loudest treatment group. Therefore, the high-amplitude treatment is in the upper range of what breeding zebra finches would experience in our aviary and is within the bounds of environmental noise that we recorded in breeding sites. Although this high-amplitude level is above the average noise that some species experience in the field (e.g. Slabbekoorn & Peet 2003; Brumm 2004), even temporary masking of male calls could have effects on male and female behaviour.

The day before each female's first preference trial, she was acclimated to the central chamber of the preference apparatus in a 40-min trial with no stimulus males present and no white noise played through the speakers. The next day, she experienced a preference trial in which she was placed in the central chamber with her pair-bonded male in one of the male stimulus cages (randomly left or right) and an arbitrarily selected extrapair male, who was the pair-bonded male of another female in the experiment, in the opposite stimulus cage. We ensured that the extrapair male had not been in previous visual or auditory contact with the test female. For each female, the same two males were used in all three environmental noise treatments. Because each extrapair male also appeared as a pair-bonded male for another female later in the experiment, we balanced morphological differences between males for each condition (i.e. as a pair-bonded male or as an extrapair male).

Immediately before the placement of the female, we began the appropriate white noise treatment. Once the female was in place, the experimenter left the room and allowed the female and males to interact for 40 min. After this period, the experimenter re-entered the room, switched

the positions of the two males to minimize any female side preferences, and allowed the trial to run for another 40 min. All activity in the acclimation and preference trials was recorded using video cameras so that we could determine the number of courtship hops performed by the males and females, as these hops are indicative of copulation solicitations, mate preference and actual mate choice (Swaddle & Cuthill 1994; Swaddle 1996; Zann 1996; Hunt et al. 1997, 2001). A courtship hop was defined as a short lateral movement either on the closest perch to a male or a hop between the closest and next closest perch to a male. During these movements, females turned their head and/or tail towards the male and often showed tail flicking, all of which are indicative of active courtship (Zann 1996). All hop counts were recorded blind with regard to treatment groups and bird identities.

Each female and her associated males experienced preference trials on consecutive days until they were exposed to all three noise treatments. Between trials, all females and males were returned to their pair breeding cages. Hence, pair bonds were not permanently broken at any stage of the experiment. All experimental procedures were approved by our Institutional Animal Care and Use Committee and followed the ABS/ASAB Guidelines for Use of Animals in Research. Following the experiment, the birds were returned to their pairs and continued to breed without any detrimental signs of the noise treatments.

Using linear regression, we examined whether the number of courtship hops performed by the female was related to the number of courtship hops performed by each male. Male courtship hops were defined in the same manner as female courtship hops, because both males and females display similar behaviours in the initial stages of courtship (Zann 1996). We stored the residuals from this analysis to render an index of female preference (referred to as residual female preference) that partitioned out the general effect of variation in male visual displays. This procedure enabled us to focus on the auditory consequences of environmental white noise on female preferences.

We tested whether the white noise amplitude treatments (low, medium, high) and the pair status of males (pair-bonded or extrapair) affected residual female preference in a full factorial repeated measures ANOVA with both noise treatment and male pair status as within-individual factors. We performed a repeated measures ANOVA to explore how male display hops were affected by the amplitude of white noise and the pair status of males. For both ANOVA models, the data satisfied assumptions of normality and homogeneity of variance. All statistical analyses were performed with SPSS version 13.0 (SPSS Inc., Chicago, IL, U.S.A.) employing two-tailed tests of probability.

RESULTS

Males did not alter their frequency of courtship hops as the amplitude of environmental white noise increased ($F_{2,38} = 1.57$, $P = 0.221$). However, males did perform more courtship hops when they appeared in the experiment as extrapair males than when they appeared as

pair-bonded males ($F_{1,19} = 7.43$, $P = 0.013$), which may help explain why Swaddle et al. (2006) found that extrapair males were more attractive to female zebra finches under intermediate noise levels.

The number of courtship hops performed by a female towards a particular male in each trial was highly positively related to the amount of courtship hopping that the male performed (female hops = $0.836 \times$ male hops - 1.91, $r^2 = 0.521$, $F_{1,118} = 128.23$, $P < 0.001$). The residuals from this regression analysis rendered an index of residual female preference, partitioning out the general relationship of female courtship with the extent of male courtship. The environmental white noise treatments did not affect the extent of residual female preference of males across the experiment (i.e. no main effect of noise treatment on residual female preference: $F_{2,38} = 2.78$, $P = 0.075$), although there was a tendency for more overall courtship in the lowest amplitude noise treatment (Fig. 2).

The status of stimulus males as either pair-bonded or extrapair males had a large effect on residual female preferences (i.e. a significant main effect of male status on residual female preference: $F_{1,19} = 17.74$, $P < 0.001$). Males were generally preferred when they were the pair-bonded partners of the choosing female (Fig. 2). The strength of preference for the pair-bonded partner was significantly affected by the amplitude of the white noise treatment (i.e. a significant noise by male status interaction on residual female preference: $F_{2,38} = 3.32$, $P = 0.047$; eta-square (effect size) = 0.149). As the amplitude of white noise increased to the highest level, the preference for the pair-bonded male significantly eroded (a priori contrasts: low versus medium noise: $F_{1,19} = 0.001$, $P = 0.998$, eta-square < 0.001 ; low versus high noise: $F_{2,38} = 4.80$, $P = 0.041$, eta-square = 0.202; Fig. 2). However, the pair preference did not invert and result in a preference for extrapair males under the high-amplitude noise treatment.

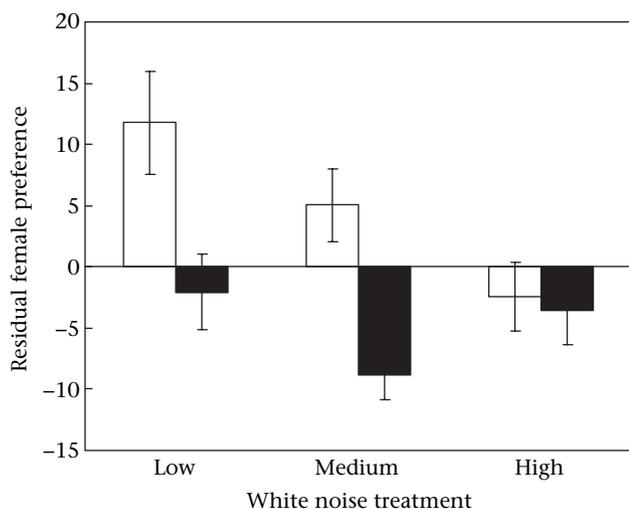


Figure 2. Mean \pm SE residual female preference for their pair-bonded male (\square) or the extrapair male (\blacksquare) in the three white noise amplitude treatments.

DISCUSSION

Our results generally corroborate previous reports of pair preferences in zebra finches and indicate that females consistently prefer their pair-bonded partner over an extrapair male in dichotomous preference trials (Clayton 1990). Preference for their pair-bonded male could result from the presence of the pair bond and/or because of the females' familiarity with those particular males compared with the novel, extrapair males (Caryl 1976). In the current study design, we cannot distinguish between these two explanations. However, it is clear that, in situations of low-amplitude environmental white noise that allow for extensive auditory and visual contact between males and a choosing female, female zebra finches consistently prefer their pair-bonded male over a novel extrapair male. This observation is wholly consistent with the strong pair bonds that are commonly reported among pairs of zebra finches (Silcox & Evans 1982; Zann 1996; Adkins-Regan 2002; Remage-Healey et al. 2003; Tomaszycycki & Adkins-Regan 2006).

The strong pair preferences did not hold as the amplitude of environmental noise increased. As the amplitude of white noise increased, the extent of preference for the pair-bonded male significantly decreased until there was no discernible preference for the pair-bonded males over the extrapair males in the high-amplitude noise treatment. This erosion of preference could not be fully accounted for by a general decrease in overall courtship activity, because residual female preference was not significantly affected by the main effect of white noise treatment. Interestingly, we did not find that females significantly preferred extrapair males over their pair-bonded males in the high-noise treatment, as predicted from a previous study (Swaddle et al. 2006). The discrepancy was not explained by analysing female courtship data without controlling for male rates of courtship; we obtained qualitatively similar results however we analysed the data. It may be relevant that the physical apparatus was different between the two studies, as was the pool of females studied, either of which could contribute to variation between the two studies. Notwithstanding these differences, the erosion of females' preferences for pair-bonded males is consistent with both studies.

We propose two explanations for the erosion of the pair preference. First, there could be a simultaneous decrease in the perceived attractiveness of the pair-bonded male and an increase in attractiveness of the extrapair male, caused by the masking of auditory cues. Overall, male courtship hopping did not change significantly with increasing amplitude noise. Therefore, we do not have evidence that males adjusted their courtship hopping to the increased noise. We did not record measures of male song output, which would have been revealing in helping to explain how males adjusted to the increased amplitude noise. We plan to perform such investigations in the future. Studies of other species suggest that males probably modulate their songs in response to increased amplitude noise (reviewed in Patricelli & Blickley 2006). When males appeared as extrapair individuals in the present study, they performed more courtship hops. Therefore,

with the masking of auditory cues in the high-amplitude noise treatment and, presumably, the greater reliance on visual cues, extrapair males may appear relatively more attractive than pair-bonded males.

Our second explanation for the decrease in pair preference is that female zebra finches may not be able to recognize individual males when auditory cues are masked by high-amplitude environmental noise (Miller 1979; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006). We do not have a direct way of assessing the likelihood of this explanation and it may be that the high-amplitude noise fundamentally affected females' abilities to recognize their mates. However, there is some evidence that males may have been able to recognize females throughout the experiment, even under the conditions of the high-amplitude noise treatment. Males increased their courtship rate when they appeared as extrapair males relative to their rate when they appeared as pair-bonded males (even under high-amplitude noise). For them to recognize that they were in the extrapair situation, males probably recognized that they were courting either their pair-bonded female or a novel, extrapair female. Individual recognition is possible in some songbirds even under conditions of noise pollution (Appeltants et al. 2005). Therefore, it is possible that females still recognized their pair-bonded male under the louder noise treatments.

No matter what proximate mechanism underlies the observation that pair preferences are eroded under higher-amplitude environmental white noise, our results have some interesting implications for the mating system of zebra finches. Although we do not have direct information, because we did not measure longer-term changes to pair bonds or actual rates of extrapair mating, our results suggest the intriguing scenario that extrapair behaviours (e.g. EPP) can be increased under situations of greater environmental noise pollution, because pair bonds are eroded. This idea would explain why zebra finches typically show low rates of EPP in nature (Birkhead et al. 1990; Zann 1996), but can have increased rates in captive situations with considerable noise and high bird density (Burley et al. 1996). At this stage, our hypothesis is speculative, but environmental noise pollution could be an additional, nonadaptive factor that affects within-species variation in rates of EPP.

Environmental noise has already been implicated as a factor affecting the behavioural modulation and evolutionary adaptation of songs and calls in adult and nestling passerines (Klump 1996; Cynx et al. 1998; Pytte et al. 2003; Rabin et al. 2003; Slabbekoorn & Peet 2003; Aubin 2004; Brumm 2004; Brumm & Slabbekoorn 2004; Fernández-Juricic et al. 2005; Leonard & Horn 2005; Patricelli & Blickley 2006; Warren et al. 2006; Wood & Yezerinac 2006). Environmental noise may also affect breeding in these birds (Reijnen et al. 1997; Patricelli & Blickley 2006; Warren et al. 2006; Wood & Yezerinac 2006). In addition, we propose that environmental noise pollution may affect fundamental aspects of the mating system of some songbirds (and perhaps other vocal species), especially those that rely on auditory signals to establish and maintain pair bonds and mate preferences (e.g. Schwartz et al. 2001; Wollerman & Wiley 2002; Brumm 2004; Kumar

2004; Mota & Depraz 2004; Warren et al. 2006; Wood & Yezerinac 2006). Therefore, in areas with higher noise pollution, the mating system of sensitive species and, consequently, the strength of sexual selection and genetic structure of the population could be affected. Our investigation indicates there are many interesting follow-up studies that could be conducted, in both experimental and field situations, to explore further the ecological and evolutionary consequences of noise pollution.

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