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Acoustic experience shapes female mate choice in field crickets

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Female choice can drive the evolution of extravagant male traits. In invertebrates, the influence of prior social experience on female choice has only recently been considered. To better understand the evolutionary implications of experience-mediated plasticity in female choice, we investigated the effect of acoustic experience during rearing on female responsiveness to male song in the field cricket *Teleogryllus oceanicus*. Acoustic experience has unique biological relevance in this species: a morphological mutation has rendered over 90 per cent of males on the Hawaiian island of Kauai silent in fewer than 20 generations, impeding females' abilities to locate potential mates. Females reared in silent conditions mimicking Kauai were less discriminating of male calling song and more responsive to playbacks, compared with females that experienced song during rearing. Our results to our knowledge, are the first demonstration of long-term effects of acoustic experience in an arthropod, and suggest that female *T. oceanicus* may be able to compensate for the reduced availability of long-range male sexual signals by increasing their responsiveness to the few remaining signallers. Understanding the adaptive significance of experience-mediated plasticity in female choice provides insight into processes that facilitate rapid evolutionary change and shape sexual selection pressure in natural populations.

Keywords: acoustic experience; mate choice; phenotypic plasticity; rapid evolution; sexual selection; *Teleogryllus oceanicus*

1. INTRODUCTION

Genetic models of sexual selection predict that female mate choice can drive the exaggeration of secondary sexual characters in males (Lande 1981; Parker 1983; Andersson 1994). However, a number of non-genetic factors affecting female choice have captured the attention of researchers owing to their potentially large effects on the strength and direction of sexual selection. These include mate search costs, female condition, predation risk, novel male effects and female search strategy (Janetos 1980; Bakker & Milinski 1991; Hedrick & Dill 1993; Widemo & Sæther 1999; Cotton *et al.* 2006). Prior social experience has also been shown to affect the outcome of female mate choice in vertebrates (Bakker & Milinski 1991; Rosenqvist & Houde 1997; Galef & White 2000; Slagsvold *et al.* 2002; Magurran & Ramnarine 2004), but this idea has only recently gained traction in invertebrate research (Wagner *et al.* 2001; Hebert 2003; Dukas 2005; Fincke *et al.* 2007; Hebert & Vink 2007).

Plasticity in female mate choice is expected to influence the rate of male trait evolution (Chaine & Lyon 2008), and the aim of our study was to better understand how social experience mediates such plasticity, thereby influencing evolutionary change in wild populations. We considered two unresolved questions. First, what properties of social experience affect female behaviour in the context of mate choice? Until now, it has been difficult to distinguish between tactile, olfactory, visual or auditory influences during pre-mating experience in invertebrates

(Koudele *et al.* 1987; Hebert 2003; Fincke *et al.* 2007). Second, what are the evolutionary consequences if social experience does affect mate choice? To our knowledge, there are few clear examples of how experience-mediated plasticity in mate choice affects the evolutionary dynamics of a rapidly evolving natural system.

We capitalized on a study system in which prior social experience might have unusually significant evolutionary consequences. Male Polynesian field crickets, *Teleogryllus oceanicus*, normally produce a calling song by rubbing their forewings together. The call attracts females for mating. However, a morphological mutation has evolved in response to an acoustically orienting predator, the fly *Ormia ochracea*, and recently swept through a *T. oceanicus* population on the Hawaiian island of Kauai. In fewer than 5 years (approx. 16–20 generations), over 90 per cent of male crickets on Kauai now exhibit a flatwing morphology that renders them mute (Zuk *et al.* 2006; Tinghitella 2008). Lacking the wing structures normally used to produce sound, these males appear to adopt a satellite strategy by intercepting females responding to the few remaining callers (Cade 1980; Zuk *et al.* 2006). The mutation probably persists owing to the advantage silent flatwing males enjoy against the parasitoid fly. The increased abundance of flatwing males has rapidly and dramatically altered the acoustic environment that individuals on Kauai experience; silence or near-silence now predominates on Kauai, as the vast majority of males cannot produce song.

In this study, we investigated how females were able to accommodate the abrupt loss of the male sexual signal to which they normally respond. Male calling song is the only known signal available to females to locate sexually

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receptive males from a distance; gryllids do not produce long-range pheromones (Tregenza & Wedell 1997) and individuals are typically spaced at least 1 m apart in the field. The population continues to thrive, however. We hypothesized that the acoustic environment in which females develop mediates plasticity in female mate choice, and that this plasticity helped to accommodate the loss of male song. In the laboratory, we manipulated females' acoustic experience during rearing to test whether females reared in silent conditions mimicking Kauai would be more responsive to male song, better enabling them to locate the few singing males that remain or flatwing satellite males in close proximity.

2. MATERIAL AND METHODS

(a) Study organisms

A *T. oceanicus* laboratory colony was established using eggs from approximately 25 females collected on Kauai in 2006. We allowed four generations to elapse prior to the start of the experiment to avoid maternal effects. All crickets were reared in silence in 15 l containers in a 25°C incubator until sex differences became apparent during their fourth instar, whereupon we transferred them to individual 118 ml plastic containers. Crickets were provided with Fluker's cricket food, Purina rabbit food and water twice weekly.

(b) Acoustic environments

We separated the fourth instar females into one of two acoustic environments: 'No Song' or 'Song'. Each environment consisted of an identical 25°C Precision 818 incubator on the same photo-reversed 12 L : 12 D cycles.

In the No Song incubator, the individually housed females remained in silence until we tested them. In the Song incubator, females were individually housed in an identical fashion but were exposed to male calling song broadcast from Sony SRS-M30 speakers during the dark phase of the light : dark cycle, when *T. oceanicus* is active.

Teleogryllus oceanicus song contains a trill-like long chirp followed by a series of paired pulses; the proportion of long chirp in a song is an important parameter evaluated by females during mate choice (Simmons *et al.* 2001; Simmons 2004; Bailey 2008). In the Song incubator, we broadcast six song models containing 0, 20, 40, 60, 80 and 100 per cent long chirp, each from a separate speaker. We broadcast all six song models simultaneously to approximate a wild setting, in which females are exposed to variation in male calling song. Females' positions in the Song incubator were randomly rotated every day to ensure that they were exposed to all song models during rearing. Females in the No Song environment were similarly manipulated on a daily basis to minimize handling differences between the treatments.

The sound pressure level in the Song incubator was adjusted to 80–85 dB at the lid of the containers. A pilot study showed that the plastic lids have an acoustic impedance of 10 dB but do not affect the peak carrier frequency or temporal components of *T. oceanicus* song transmitted through them (see the electronic supplementary data). Thus, song intensities experienced by female crickets in the Song environment ranged from 70 to 75 dB, which are typical of a male cricket singing from a distance of 50 cm (Simmons *et al.* 2001).

We took measures to decrease the likelihood that micro-environmental properties of the incubators differentially affected female behaviour. Incubators were cleaned with 10 per cent bleach solution before the experiment to eliminate residual pathogens. The incubators produced the same level of background white noise (53 dB). Each female was individually housed, and therefore separated from the environment within the incubator, with the exception of acoustic cues and the small amount of air that passed through the holes in the container lids. Finally, a previous study assessed mate choice behaviour in the same population, using females reared in either of the incubators ($n=10$ for each incubator; Bailey 2008). None of the components of mate choice (discrimination, responsiveness and preference) differed between the two incubators (all $p>0.11$).

(c) Time frame

Female *T. oceanicus* become sexually responsive 4–5 days after eclosion (N. Bailey 2008, personal observation). To gauge female responsiveness during the most biologically realistic time frame possible and avoid age-related variation in responsiveness (Prosser *et al.* 1997; Gray 1999), we tested all adult females at 6 days post-eclosion. Testing all females at an early stage also diminished the possibility of confounding habituation effects: females in the Song environment might show reduced response effort in subsequent tests, if they had grown accustomed to being unable to contact singing males. We minimized any habituation effects by performing phonotaxis trials just after the onset of sexual receptivity (Sakaluk 1982). Finally, the effects of recent exposure to song, 'prior male' effects, have been documented in other cricket species, and can influence subsequent mating decisions at least 20 min after exposure (Wagner *et al.* 2001). We therefore removed females from the Song environment and kept them acoustically isolated for a single light cycle; all crickets experienced a minimum of 16 hours of undisturbed silence prior to testing.

(d) Phonotaxis trials

We assessed female responsiveness by conducting a single phonotaxis trial at 25°C under red light with each female. We tested 150 females from the No Song treatment and 150 females from the Song treatment, and within each treatment, we tested 25 females with each song model. The 0 and 100 per cent song models exceed the normal range of variation in the wild, but were included to test the entire range of possible male trait values. Females were tested only once. The cross-sectional design mitigated the known effects of immediate prior acoustic experience on female phonotaxis behaviour that would have confounded our measures of responsiveness if we repeatedly tested each individual (Wagner *et al.* 2001).

A single female was placed 293 cm from the end of a rectangular chamber lined with acoustic foam (305×28×29 cm), and a plastic container 11 cm in diameter was carefully inverted over her. She was allowed to rest in silence for 2 min, after which we simultaneously lifted the container and began playback of one of the six song models from a speaker at the opposite end of the chamber. The playback intensity was 60 dB at the point of release, which approximated the intensity of a cricket singing at the distance of the speaker. Disturbance to females

Table 1. Three-way *G*-test of independence exploring how acoustic rearing environment (Song versus No Song) and playback song model affected the proportion of females exhibiting positive phonotactic responses. (Significant *p*-values are indicated in italics.)

	d.f.	<i>G</i>	<i>p</i>
overall <i>G</i>	16	50.06	<0.001
acoustic environment	1	33.63	<0.001
song model	5	7.06	0.008
acoustic environment \times song model	5	8.88	0.114

Table 2. GLMs exploring how acoustic rearing environment (Song versus No Song), playback song model and the interaction between the two affected female crickets' response latency, time of first movement and distance to the speaker. (Significant *p*-values are indicated in italics.)

	d.f.	<i>F</i>	<i>p</i>
response latency			
acoustic environment	1	10.15	0.002
song model	5	0.85	0.514
acoustic environment \times song model	5	2.95	0.027
error	175		
time of first movement			
acoustic environment	1	4.83	0.029
song model	5	2.15	0.060
acoustic environment \times song model	5	1.50	0.190
error	264		
distance to speaker			
acoustic environment	1	3.71	0.057
song model	5	1.08	0.378
acoustic environment \times song model	5	0.31	0.908
error	101		

was negligible during all portions of the trial, which lasted 5 min.

We measured the following four characteristics of female responsiveness: (i) latency to initiate any walking movement after playback began, (ii) whether or not a female moved towards and touched the speaker at the opposite end of the chamber during the 5 min (positive versus negative response), (iii) response time if the response was positive and (iv) distance from the playback speaker at the end of the trial if the response was negative. Females that settled closer to a singing male may be more likely to eventually respond to him in wild situation, where they are not limited to a 5 min response period, and may also encounter flatwing satellites that have responded to the singing male.

(e) Analysis

We tested the effects of acoustic experience and song model on the proportion of females responding positively to playbacks using a three-way *G*-test of independence (Sokal & Rohlf 1969). General linear models (GLMs) were used to test the effects of acoustic environment on movement latency in all crickets ($n=276$), response latency in those that positively responded ($n=187$) and

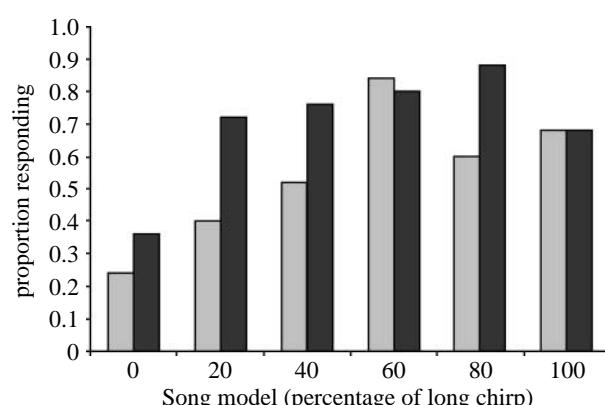


Figure 1. Likelihood that females positively responded to calling song playbacks. Females exposed to song (Song) during rearing are represented by grey bars, and those reared in silence (No Song) by black bars. Each female was tested with one of six song models varying in the proportion of long chirp (0–100% long chirp); a positive response was scored if the female moved to the end of the testing arena and touched the playback speaker before the end of the 5 min trial.

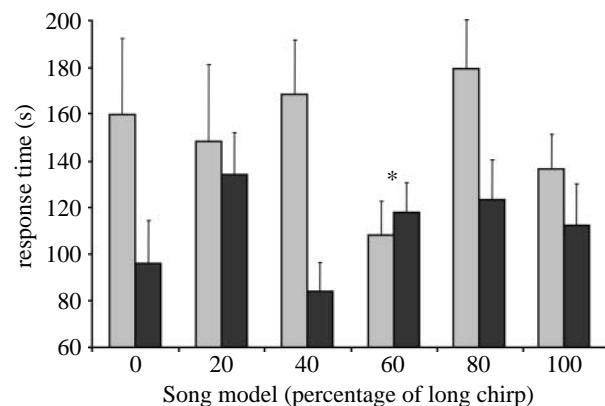


Figure 2. Female response latencies. Females exposed to song (Song) during rearing are represented by grey bars, and those reared in silence (No Song) by black bars. Response latency directly reflects the amount of time a female takes to reach an acoustic stimulus starting from the time it is perceived; females with shorter response latencies are interpreted to be more responsive. The asterisk highlights the 60 per cent long-chirp song model that has been shown to be the most preferred song model in population-wide preference tests (Bailey 2008). Bars indicate 1 s.e.

distance moved in those that did not ($n=113$). Size did not covary with any of the measures of responsiveness (all $p \geq 0.365$), so we did not include it as a covariate in the analyses. All distance and latency data were natural log transformed to ensure normality. Analyses were performed in MINITAB v. 12.21 and JMP v. 6.0.

3. RESULTS

(a) Acoustic experience decreased responsiveness

Females from Kauai reared in a silent environment mimicking the current situation in the field were more responsive to male song than females from the same population reared in an environment in which they were exposed to biologically realistic levels of male calling song (tables 1 and 2, figures 1–3).

All aspects of female responsiveness were affected in a parallel manner by acoustic experience: silent rearing conditions increased both the likelihood and speed of

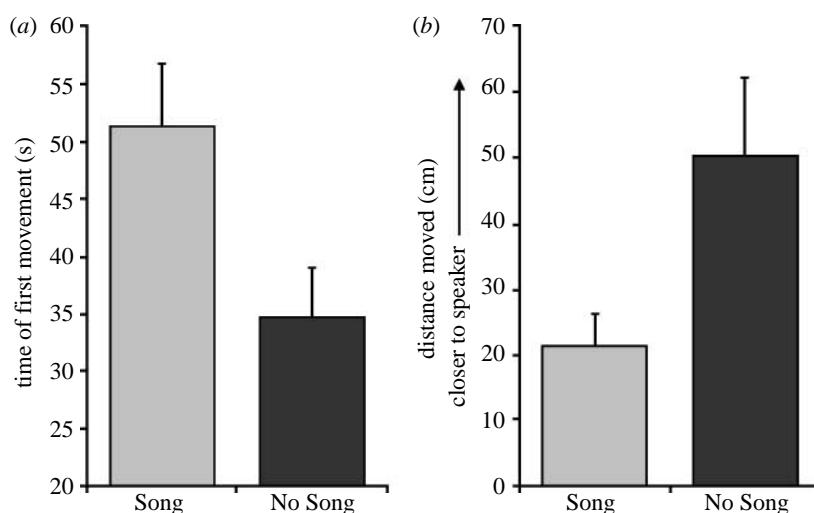


Figure 3. (a) Latency of the first movement for all crickets tested and (b) distance moved from the starting point for all females that did not respond positively during the trial. Bars indicate 1 s.e.

females moving to a source of male calling song. Overall, females were less likely to respond positively to a playback if they had been exposed to song during rearing (table 1, figure 1). Of the females that did respond, those exposed to song during rearing took longer to reach the speaker during playbacks (table 2, figure 2). Crickets also took longer to initiate walking behaviour, if they had experienced song during rearing, and of the females that did not respond positively during playback tests, those reared in silence showed a marginally non-significant trend towards moving closer to the speaker by the end of their 5 min trial, compared to those exposed to song during rearing (table 2, figure 3).

(b) Acoustic experience increased discrimination in responding females

Females exposed to song during rearing were more discriminating of male song. A significant interaction between song model and acoustic environment indicated that the effect of acoustic environment on response latency was not consistent for all song models (GLM: $F_{5,175}=2.95$, $p=0.027$). Overall, females previously experiencing song showed reduced response latencies compared to those reared in silence, but females from both treatments responded rapidly when presented with the one song model that is known from previous work to be the most preferred by Kauai females: the 60 per cent long chirp model (Bailey 2008; figure 2). A *post hoc* comparison revealed that the 60 per cent long chirp model significantly contributed to the interaction between acoustic environment and song model ($t_{5,175}=2.56$, $p=0.011$). Thus, females responded rapidly to the most preferred song, regardless of their acoustic experience. The proportion of females from the two acoustic environment treatments that positively responded to playbacks did not differ depending upon the song model tested (G -test, $G_5=8.88$, $p=0.114$).

4. DISCUSSION

Acoustic experience in the absence of any other social cues was sufficient to alter female mate choice in *T. oceanicus*. Females that heard male calling song during

rearing were less responsive to song during playback tests, but exercised greater discrimination. Several authors have advanced the idea that experience with potential mates may actually be required for the choosy sex to develop preferences. For instance, in a mixed population of brush-legged and non-ornamented wolf spiders (genus *Schizocosoma*), juvenile females exposed to either type of male later displayed strong preferences for brush-legged males, whereas unexposed females showed no preference (Hebets & Vink 2007). Similarly, male damselflies (*Enallagma civile*) showed learned sensory biases towards female morphs to which they had been previously exposed, whereas those reared in solitude showed no preference (Fincke *et al.* 2007).

Here we used six different song models to gauge whether or not the effect of acoustic environment was consistent across all values of the male trait, potentially indicating interactions between acoustic rearing environment and mating preferences exerted by females. The models varied in a single parameter that has been demonstrated to be important in *T. oceanicus* mating decisions (Simmons *et al.* 2001). Females from both treatments responded rapidly when presented with the one song model that is known from previous work to be the most preferred by females from this population (Bailey 2008; figure 2). Thus, females experiencing song during rearing were slower to respond to male song, unless it was the most preferred song. By contrast, females reared in silence did not appear to discriminate as strongly against non-preferred songs. This corroborates Hebets & Vink's (2007) observation, but instead of acoustic experience driving the development of preference, it seems more plausible that the lack of experience drives indiscriminate mating responses in *T. oceanicus*. Females may have pre-existing preferences, but only exercise them when they perceive that enough males are available to choose from, by altering their threshold of mate acceptance or by sampling more males, depending upon their search strategy.

The adaptive significance of behavioural plasticity has often been considered in the context of coping with a new or abruptly altered environment (Losos *et al.* 2000; Price *et al.* 2003; Ghalambor *et al.* 2007). Selection is expected

to favour individuals that can accommodate variation in environmental constraints and selection pressures through behavioural flexibility or learning (Wcislo 1989; West-Eberhard 2003). On Kauai, the population of field crickets is unique because their environment changed as a direct result of a phenotypic modification of the crickets themselves. Evidence from our laboratory study strongly supports the idea that phenotypic plasticity in mate choice, mediated solely by the acoustic environment, allowed female crickets to compensate for the reduced availability of singing males on Kauai by responding more readily, more quickly, and with less discrimination to the few calling males that remain in the population. As silent flatwing males appear to act as satellites to the few remaining callers (Zuk *et al.* 2006), females responding to the same signal are more likely to encounter and mate with a silent flatwing or the calling male himself.

The future trajectory of the Kauai population remains to be seen. Theoretical and empirical studies have shown that female responsiveness can affect the strength of sexual selection on male traits (Lande 1981; Butlin 1993; Ritchie *et al.* 2005), and the relative strength of sexual selection on male song exerted by female choice may be relaxed in the Kauai population owing to indiscriminately responding females. In addition, declines in one component of female choice, such as responsiveness, may diminish the effects of other components such as preference or discrimination (Gilburn & Day 1999; Bailey 2008). If negative frequency-dependent selection on the male morph leads to fluctuations in the proportion of flatwings in the population, then the acoustic environment females perceived in the field will similarly fluctuate. Since acoustic experience during rearing appears to shape female choice, sexual selection on male song may be periodically relaxed, in turn maintaining greater genetic variation for male song than would be expected in a normal population. A recent study of lark buntings supports this idea. Chaine & Lyon (2008) found that temporal flexibility in female preferences was adaptive, and dampened sexual selection on male traits. The potential for predictable changes in sexual selection pressure on male calling song makes continued monitoring of the *T. oceanicus* population on Kauai a priority for future studies.

It is somewhat surprising that acoustic rearing environment in and of itself was sufficient to modify female behaviour in *T. oceanicus*. Mating history and olfactory cues have been shown to affect female responses (Cade 1979; Koudele *et al.* 1987; Bateman 2001; Bateman *et al.* 2004), but to our knowledge, our results are the first demonstration that acoustic stimuli produce long-term effects on mate choice in an insect. Acoustic experience affected female responsiveness well after the completion of a full light cycle (over 16 hours), suggesting that acoustic effects persist beyond the previously recognized ‘prior male’ effects in other invertebrates (Wagner *et al.* 2001). Complex learning and memory capabilities are thoroughly documented in many insect groups, especially in the context of other behaviours such as foraging (Dukas 2004, 2005; Worden & Papaj 2005), and our results open the door to areas of future research investigating the behavioural basis of rapid evolution and the maintenance of genetic variation in traits under strong sexual selection.

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Correction

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Social personality trait and fitness

J. Cote, A. Dreiss and J. Clobert

In **table 1** of Cote *et al.* (2008), the table title contains incorrect significance values. The symbols (${}^{\#}p < 0.10$, ${}^{*}p < 0.05$) in the legend of **table 1** did not match with those (${}^{*}p < 0.10$, ${}^{\#}p < 0.05$) in the table. Thus, all the significant results ($p < 0.05$) appeared non-significant ($p < 0.10$).

It is now presented correctly as:

Table 1. Effects of population density and social tolerance at birth on fitness outcomes (estimates are given for high-density populations $D+$). (${}^{\#}p < 0.10$, ${}^{*}p < 0.05$.)

factors	survival		body growth		gravidity	
	estimates \pm s.e.	test statistics	estimates \pm s.e.	test statistics	estimates \pm s.e.	test statistics
density ($D+$)	0.39 ± 0.38	$F_{1,14}=1.01$	-2.04 ± 0.98	$F_{1,13}=4.26^{\#}$	-0.51 ± 1.28	$\chi_1=0.16$
social tolerance	-0.001 ± 0.001	$F_{1,133}=0.08$	0.003 ± 0.001	$F_{1,43}=5.68^{*}$	0.005 ± 0.003	$\chi_1=4.05^{*}$
density \times tolerance	0.003 ± 0.001	$F_{1,133}=4.01^{*}$	-0.003 ± 0.003	$F_{1,42}=1.11$	-0.07 ± 0.09	$\chi_1=0.85$
date of birth	0.027 ± 0.035	$F_{1,132}=0.63$	-0.13 ± 0.08	$F_{1,43}=3.05^{\#}$	-0.04 ± 0.12	$\chi_1=0.12$
body length in May	—	—	—	—	0.43 ± 0.21	$\chi_1=5.83^{*}$

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Acoustic experience shapes female mate choice in field crickets

Nathan W. Bailey and Marlene Zuk

In Bailey & Zuk (2008), we inaccurately cited a previous publication (Bailey 2008) as evidence that the *Teleogryllus oceanicus* females mostly preferred the 60% long-chirp male song model in mate choice playback tests. The previous publication does not explicitly indicate the most preferred song model. However, this does not affect the results or the interpretation in Bailey & Zuk (2008). The key point is that the female crickets reared in the ‘song’ environment mostly preferred the 60% long-chirp male song model, which is evident from **figure 1**. The rationale and conclusion that the discrimination was increased among ‘song’ crickets therefore remains the same: females that experienced song during rearing responded rapidly only to their most preferred song model, whereas the females reared in silence responded rapidly to all song models. We have also resupplied a corrected version of **figure 1**. Two bars (the 40 and 60% ‘no song’ bars) were accidentally transposed when the original graph was created, but neither the data, the statistical results nor our interpretation are affected.

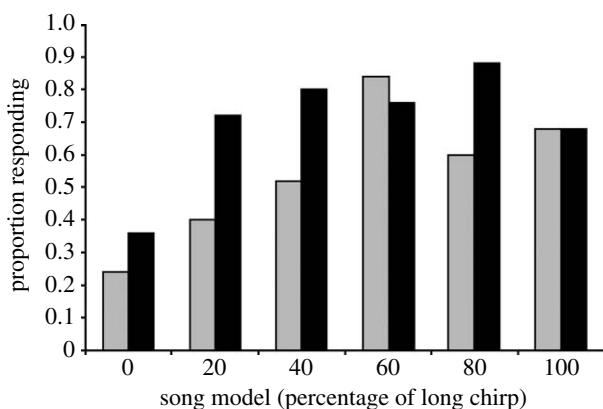


Figure 1. Likelihood that females positively responded to calling song playbacks. Females exposed to song (Song) during rearing are represented by grey bars, and those reared in silence (No Song) by black bars. Each female was tested with one of six song models varying in the proportion of long chirp (0–100% long chirp); a positive response was scored if the female moved to the end of the testing arena and touched the playback speaker before the end of the 5 min trial.

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