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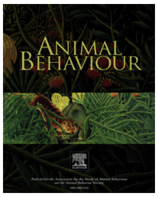

Is plasticity in field cricket mating behaviour mediated by experience of song quality?

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Many animals rely upon signals to discriminate among potential mates. Through mate choice, they may gain fitness advantages for themselves and their offspring and exert selection on signals and signallers. In some species, mating preferences are phenotypically plastic and mediated by experience of signals. *Teleogryllus oceanicus*, the Pacific field cricket, has been a productive model for studies of acoustically mediated phenotypic plasticity because many aspects of adult mating behaviour and reproductive physiology are differentially expressed when crickets develop in the presence versus absence of conspecific signals. An open question is whether the quality of conspecific signals experienced during development also mediates the mating preferences of adult females, as it does in some other animals. We tested the mating assurance in a variable environment hypothesis, which posits that adaptive plasticity in the expression of female mating preferences could protect females from costs associated with being too selective when preferred mates are rare or absent, while allowing selectivity when preferred mates are available. We experimentally manipulated the acoustic signals in the rearing environment as a reliable cue about the availability of preferred mates in the adult environment. Specifically, environments varied in the percentage of long chirp, a trait of male advertisement song known to be under precopulatory sexual selection. When subjects reached maturity, we used a within-subjects phonotaxis (movement towards sound) assay to measure female preferences for the percentage of long chirp. We replicated our experiment in populations from three islands of the Hawaiian Archipelago. We found evidence that some measures of female response are plastic and mediated by song quality, but effects were population specific and not entirely consistent with the predictions of the mating assurance in a variable environment hypothesis. Our results point to limited song quality-mediated plasticity in female mating preferences.

In many animal species, individuals discriminate among potential mates on the basis of sexual signals, such as calls or songs, colourful plumage, or odours (Andersson, 1994; Bradbury & Vehrencamp, 2011; Gerhardt & Huber, 2002). Mate choice based on sexual signals can provide fitness benefits for the chooser and its offspring (Andersson, 1994; Maynard Smith & Harper, 2003). As a result, receivers often have strong preferences for the characteristics of signals and, through mate choice, exert sexual selection on signals and signallers (Andersson, 1994; Maynard Smith & Harper, 2003; Rosenthal, 2017). Receiver preference functions, which measure receiver interest for a range of signal characteristics, are often measured and used to infer the strength and shape of sexual selection on sexual signals (Gerhardt & Brooks, 2009; Gerhardt et al., 2000; Klappert & Reinhold, 2003; Murphy & Gerhardt, 2000; Oh & Shaw, 2013; Reichert & Ronacher, 2015; Tanner et al., 2017). However, the existence of receiver mating preferences does not guarantee that receivers exercise mate choice in nature. Many factors may prohibit or alter the expression of mating preferences, including complex phenotypes that limit choice based on individual characteristics (Bentsen et al., 2006; Brooks et al., 2005; Tanner et al., 2017), noise in the environment (Reichert & Ronacher, 2015; Tanner & Bee, 2019, 2020) and within-individual variation in signalling behaviour that masks the between-individual variation that is the target of mate choice (Tanner & Bee, 2020).

One factor that may modify or prevent expression of mating preferences is receiver experience (Bailey, 2011; Collins, 1995; Desjonquères et al., 2019, 2021; Godin et al., 2005; Swanger & Zuk, 2015). That is, mating preferences in adulthood are sometimes phenotypically plastic and shaped by prior experience of sexual signals. Female wolf spiders, *Schizocosa uetzi*, that experience male

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courtship as subadults develop a preference for males with a familiar visual signalling phenotype (Hebets, 2003). In treehoppers, receivers that were exposed during development to the songs preferred by adult females were more selective as adults than females reared in the presence of less attractive signals or silence (Fowler-Finn & Rodríguez, 2011, 2012), and both experience and practice of signalling during development affects aspects of female preference functions, including peak preference and peak responsiveness (Desjonquères et al., 2019, 2021). Female flightless bushcrickets, *Ephippiger diurnus*, reared in the presence of attractive male songs grow up to be more selective in phonotaxis trials and also invest more in reproduction by producing more eggs (Rebar et al., 2019). Phenotypic plasticity may be adaptive or nonadaptive (Ghalambor et al., 2007; West-Eberhard, 2003), but to the extent that receivers have experience-mediated plasticity in their mating behaviour, either adaptive or nonadaptive plasticity may affect signal evolution. An important aspect of understanding how sexual selection acts on signals is how the experience of sexual signals might alter receiver preferences.

The Pacific field cricket, *Teleogryllus oceanicus*, has been a particularly productive model for understanding how acoustic signals mediate phenotypic plasticity. As in other field crickets, males of *T. oceanicus* typically produce calling song that functions to attract females from a distance (Gerhardt & Huber, 2002; Huber et al., 1989). Female crickets have preferences for characteristics of male calling song and are more likely to approach and mount males with these attractive characteristics (Bentsen et al., 2006; Gerhardt & Huber, 2002; Simmons et al., 2001; Wagner et al., 1995). However, on several Hawaiian islands, populations of *T. oceanicus* are undergoing adaptive sexual signal loss: single-gene, sex-linked mutations causing the development of wings that lack song-producing structures have spread through these populations (Pascoal et al., 2014; Zhang et al., 2021; Zuk et al., 2006). Mutant males (‘flatwings’) are protected from parasitization by an acoustically orienting tachinid fly, *Ormia ochracea*, but are unattractive to female crickets, who strongly prefer singing males (Tanner, Swanger et al., 2019; Tinghitella & Zuk, 2009; Zuk et al., 2006).

Sexual signal loss in Hawaiian *T. oceanicus* has led to extensive research about how the presence versus absence of conspecific signals in the environment impacts cricket behaviour and physiology. Females raised in silence show increased responsiveness to song (Bailey & Zuk, 2008; Lierheimer & Tinghitella, 2017) and decreased investment in reproductive tissues (Heinen-Kay et al., 2019). Males raised in silence have lower sperm viability (Gray & Simmons, 2013) as well as different seminal fluid composition (Simmons & Lovegrove, 2017) and associated manipulation of female remating behaviour (Moschilla et al., 2020) and increased male mate searching and locomotor behaviours (Balenger & Zuk, 2015). These studies demonstrate that many aspects of *T. oceanicus* phenotypes are plastic and that this plasticity is mediated by song. However, because research on acoustically mediated plasticity in *T. oceanicus* has focused on manipulations of the presence and absence of song, we currently lack an understanding of whether plasticity in female behaviour is mediated by signal quality (but see Lierheimer & Tinghitella, 2017 and discussion thereof below).

Here, we used the Pacific field cricket to extend our knowledge about plasticity in receiver behaviour: does the quality, and not simply the presence or absence, of male song experienced during the late juvenile stage and early adulthood affect female mating preferences? In general, selection is expected to favour plastic phenotypes when populations experience variable environments, there exist reliable cues about the environment, phenotypes have differential success in each environment and there is no single phenotype that performs best across environments (Ghalambor et al., 2007; Kirkpatrick & Gomulkiewicz, 1992; Moran, 1992; Via et al., 1995). We tested the mating assurance in a variable environment hypothesis, which posits that plasticity in the expression of female mating preferences may be adaptive, insomuch as plasticity protects females from missed opportunity costs incurred by overselectivity in the absence of preferred mates or by overpermissiveness when mates of preferred types are widely available (Fowler-Finn & Rodríguez, 2011, 2012). The mating assurance in a variable environment hypothesis makes two main predictions. First, receivers' peak preference, that is, the phenotype with the highest attractiveness (Rodríguez et al., 2013), should be unchanged regardless of the acoustic environment experienced during development. Second, female selectivity should be mediated by experience of acoustic signals, such that females reared in the presence of more attractive signals become more selective, while females reared in the presence of less attractive signals become less selective. This is because selective females are expected to outperform permissive females in the presence of high-quality mates, but permissive females are expected to outperform selective females in the absence of high-quality mates.

In Hawaiian crickets, we also expected between-population differences in the extent of plasticity. In Wailua, Kaua‘i (hereafter, ‘Kaua‘i’), males with preferred signalling phenotypes are almost never available because very few males can sing (Zuk et al., 2018). In Hilo, Hawaii (hereafter, ‘Hilo’), preferred mates are nearly always available because nearly all males can sing and natural variation in male signal quality exists. By contrast, in Laie, O‘ahu (hereafter, ‘O‘ahu’), about half of males can sing (Pascoal et al., 2014; Zuk et al., 2018), which we expect to yield spatial and temporal variability in the presence of preferred signalling phenotypes. We thus expected O‘ahu to be the most variable environment and therefore the population most likely to select for plasticity. In populations from Kaua‘i and Hilo, plasticity in female preference expression is likely to be less important because the availability of preferred mates is more constant.

We experimentally manipulated the song quality in the acoustic environment between the late juvenile stage and attainment of sexual maturity as a reliable cue about the availability of males that sing preferred songs in the adult environment. During the acoustic experience phase, each subject experienced one of three treatments differing in the song's percentage of long chirp, a signal trait under precopulatory sexual selection (Bailey & Zuk, 2008; Simmons et al., 2001). Receivers in Hawaiian populations typically prefer percentages of long chirp above the Hawaiian average of 27% long chirp, with peak preferences for 60% long chirp (Bailey & Zuk, 2008). We measured female preferences for the percentage of long chirp using a series of single-stimulus phonotaxis tests in which we sequentially presented subjects with all three percentages of long chirp from the acoustic experience phase. We replicated the experiment in populations from Hilo, Hawaii, Laie, O‘ahu and Wailua, Kaua‘i.

METHODS

Animal Ethics Note

Invertebrates are not subject to ethical review requirements in the United States, but we nevertheless adhered to the Animal Behavior Society/Association for the Study of Animal Behaviour Guidelines for the ethical treatment of animals. The United States Department of Agriculture – Animal and Plant Health Inspection

Service granted permission to bring cricket eggs from Hawai'i to the mainland United States and maintain them in the laboratory.

Subjects and Experimental Design

Subjects were 328 adult females of *T. oceanicus* descended from wild-mated females collected from three populations, in Hilo, Hawai'i ($N = 115$), Lā'ie, O'ahu ($N = 108$) and Wailua, Kaua'i ($N = 105$) between 28 August and 16 September 2016. These populations were chosen because they differ from each other in the frequency of mutant, flatwing males (Pascoal et al., 2014; Zuk et al., 2018). While we refer to the Kaua'i and O'ahu populations by the names of the islands on which they occur, we note that the flatwing frequencies in these populations are not necessarily representative of flatwing frequencies across the entire island (Rayner et al., 2019). To establish laboratory populations from which these subjects came, we collected 20 females from each wild population. Wild females were housed in groups of 10 in 1.5-litre plastic containers with lids and given fresh vegetables ad libitum and damp cotton in which to lay eggs over 5 days and nights. Afterward, the wild females were released at their point of capture and their eggs were taken to the University of Minnesota, where they were transferred to 6-litre or 15-litre plastic containers with lids. All crickets in our experiment were kept in Caron model 6025-2 insect growth chambers (Caron Products and Services, Marietta, OH, U.S.A.) that maintained a reversed 12:12 h light:dark cycle, 26 °C and 75% humidity. All crickets were given egg cartons for shelter and cotton soaked in distilled water. Juveniles were fed Fluker's High-Calcium Cricket Diet (Fluker Farms, Port Allen, LA, U.S.A.), while adults were fed Purina Rabbit Chow (Purina, Gray Summit, MO, U.S.A.). We reared two generations of crickets in the laboratory to control for maternal effects; that is, experimental crickets were of the second-filial (F2) generation or later.

To obtain unmated female crickets with no acoustic experience of sexual signals, we isolated juvenile females as soon as they were old enough to be accurately separated by sex and prior to the penultimate instar, when their ears become functional (Ball et al., 1989). Isolated females were housed in 118 ml cups with plastic lids, randomly assigned to either the 27%, 60% or 72% long chirp treatment (see below) and immediately transferred to treatment-specific incubators that lacked live males. We applied acoustic treatments by broadcasting song during the entire dark cycle (12 h/day) to the experimental females during the late stage juvenile and early adult period.

Song Models and Acoustic Treatments

Song models were constructed de novo using custom scripts in MatLab v.2016a (Mathworks, Natick, MA, U.S.A.). To determine average Hawaiian song characteristics for song model construction, we used data set of calls recorded on all three islands in the 1990s. This data set was used in lieu of more recently collected data after exhaustive acoustic sampling across two field trips in 2016 and 2017 yielded only three recordings of normal-wing Kaua'i males; we opted to use an older data set that adequately represented all three populations rather than a newer data set that severely undersampled Kaua'i. Each male cricket was recorded singing in the field for at least 1 min using a directional microphone and a Sony Professional Walkman. From each recording, the temporal and spectral characteristics of 10 consecutive songs were measured and average trait values were calculated for each male. We temperature-corrected the data to 24 °C following the methods of Platz and Forester (1988). Song characteristics vary somewhat among geographically separate populations in *T. oceanicus* (Simmons et al., 2001). To avoid confounding population differences with stimulus differences, we decided to use the same song model for all three populations. To ensure each population was given equal weight in the Hawaiian average song model, we used a random sample of 50 recordings from each population to calculate the average trait values to be used in the synthetic stimuli. Where necessary to determine a number of discrete components to include in the signal, the population mean value was rounded to the nearest whole number.

The song of *T. oceanicus* is a multicomponent signal. The first part of the song is the 'long chirp', a trill-like series of three to nine evenly spaced pulses (Hawaiian average: 5 long chirp pulses; the black areas of the waveforms in Fig. 1). The second part of the song is a series of five to six 'short chirps', which each consist of two pulses (Hawaiian average: 6 short chirps; the grey areas of the waveform in Fig. 1). The percentage of long chirp is determined by dividing the duration of the long chirp (i.e. the time elapsed between the beginning of the first pulse and the end of the last pulse in the long chirp) by the total song duration. We chose percentages of long chirp to use in the study based on the recordings that established the mean percentage of long chirp across Hawaiian populations and previous studies of female preferences. The 27% long chirp song model was chosen to represent the global Hawaiian average percentage of long chirp; the 60% long chirp song model was chosen based on previous research that showed females prefer 60% long chirp to all other proportions tested (Bailey & Zuk, 2008); the 72% long chirp song model was chosen to give equal spacing between the three treatments in terms of the total number of pulses in the long chirp (27% = 5 pulses, 60% = 19 pulses, 72% = 33 pulses). We manipulated the percentage of long chirp in the song by adding whole numbers of pulses (and associated interpulse silent intervals) to the long chirp segment of the song (Fig. 1). The duration of the long chirp and the total song duration were allowed to change with the increasing number of pulses. Receivers show population level preferences for more pulses in the long chirp, irrespective of total song duration (Pollack, 1982; Simmons et al., 2001).

Trait values of the synthetic songs not under manipulation were assigned to Hawaiian average values, as follows. All songs had a long chirp pulse duration of 39 ms, a long chirp interpulse interval of 24 ms, a short chirp pulse duration of 30 ms, a short chirp interpulse interval of 11 ms, an interchirp interval of 69.5 ms and an interpart interval (between the end of the long chirp and onset of the first short chirp) of 27 ms. The intersong interval (between the end of the short chirps and the beginning of the next long chirp) was 72.6 ms. All pulses were generated with a centre frequency of 4853 Hz and a linear frequency-modulated downsweep with a bandwidth of 826 Hz.

Each pulse was shaped to have a species-typical amplitude envelope created using exponential functions. For the long chirp, the rise time was 22.5 ms and the pulses reached 50% of their maximum amplitudes at 45% of the rise time; the amplitude of each pulse decreased starting at 16.4 ms before the end of the pulse and pulses declined to 50% of their maximum amplitude at 62.5% of the fall time. For the short chirp pulses, the rise time was 19.7 ms and pulses reached 50% of their maximum amplitude at 33.3% of the rise time; the fall time was 12.2 ms and the pulses declined to 50% of their maximum amplitude at 79.6% of the fall time.

We used five incubators in the experiment, of which four were occupied at any one time. To control for any effects of incubator, we randomized the initial assignment of treatments to incubators and rotated the treatments through all three incubators over the course of the experiment. We also alternated which of the remaining two incubators was used as the 'quiet' incubator. We lined the walls and shelves of all incubators with 'egg-crate' mattress-topping foam to minimize acoustic artefacts. Each incubator contained one shelf

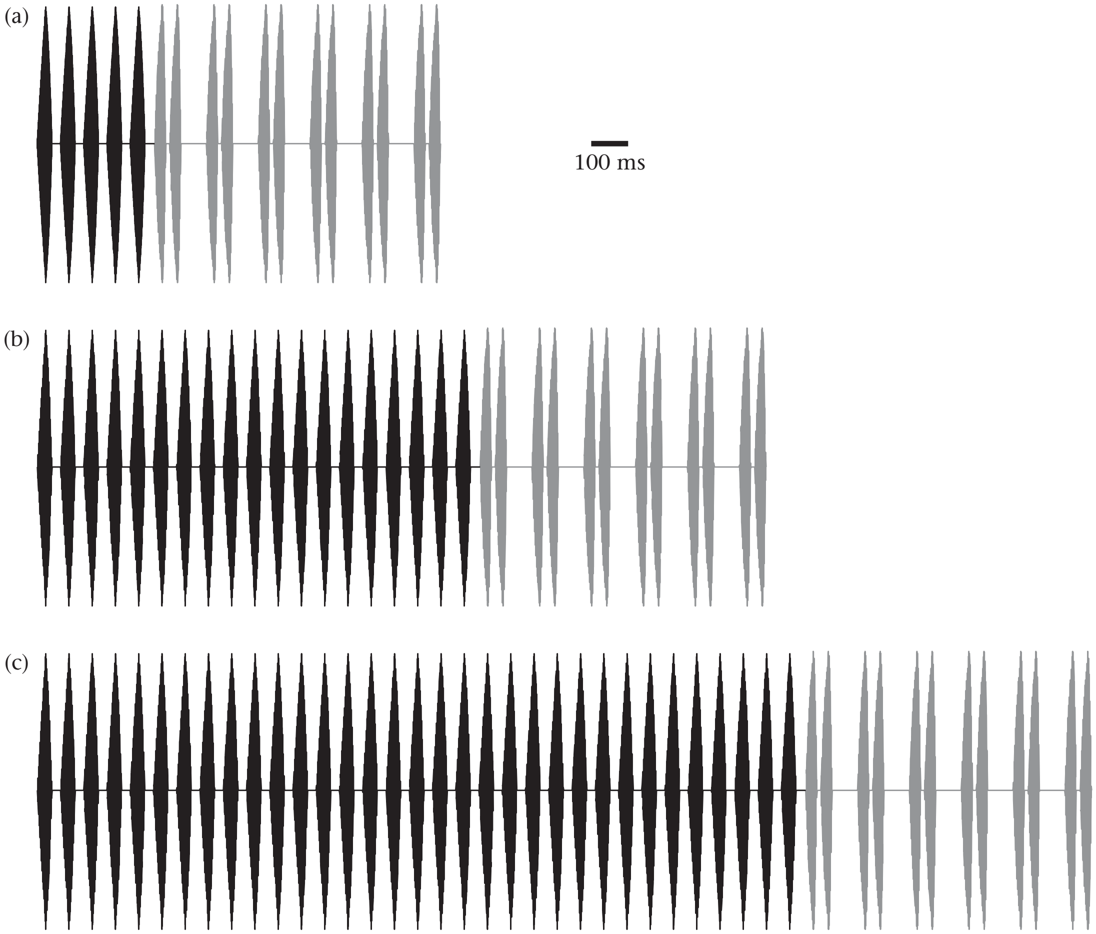

Figure 1. Waveforms of synthetic acoustic stimuli used during the acoustic treatment phase and as phonotaxis stimuli. We manipulated the percentage of long chirp by adding pulses to the long chirp (black) while keeping the number of short chirps (grey) constant. The acoustic stimuli had 5, 19 and 33 long chirp pulses, respectively, to generate (a) 27%, (b) 60% and (c) 72% long chirp songs.

that divided the top and bottom halves into two compartments, which were not acoustically isolated from one another.

In the treatment incubators, we played songs back as uncompressed WAV files from AGPTEK A20 (AGPTEK, Brooklyn, NY, U.S.A.) audio players. Two Bose SoundLink Color 2 (Bose Corporation, Framingham, MA, U.S.A.) speakers were placed in each incubator, one on each shelf. Playback was calibrated to a maximum sound pressure level between 70 and 75 dB (re. 20 μPa, fast RMS, C-weighted) across the floor of each shelf using an Extech SDL600 sound level meter (FLIR Commercial Systems, Inc., Nashua, NH, U.S.A.). This playback level was intended to approximate the level of a singing cricket at a distance of 50 cm (Simmons et al., 2001).

All isolated juveniles were checked daily for eclosion to adulthood during the acoustic treatment. We noted and tracked the date of eclosion to control effects of subject age. Throughout the acoustic treatment phase, all individuals were transferred to clean enclosures twice weekly and rotated haphazardly within the incubator to control for positional effects. On day 4 after eclosion, females were moved to a quiet incubator, which lacked both song playback and adult males, to minimize any effects of recent acoustic experience in the behavioural testing phase.

Phonotaxis Trials

Cricket receivers move towards sounds they recognize as conspecific signals and move more often and more quickly towards more attractive songs (Gerhardt & Huber, 2002; Huber et al., 1989). We thus used a phonotaxis assay to measure female preferences. To control for the effects of female age on mating behaviour (Judge et al., 2010; Mautz & Sakaluk, 2008; Moschilla et al., 2019; Tanner, Garbe et al., 2019), we randomized trial order between subjects and restricted the age window of our assay to between days 6 and 11 after adult eclosion. Each female was tested on three separate days within the window. Phonotaxis trials were carried out under red light in a semi-anechoic room at 24 ± 2 °C in a custom arena (0.5 × 1.5 × 0.5 m, width × length × height) constructed from Extruded Polystyrene Insulation (3/4 inch × 4 feet × 8 feet (1.9 cm × 1.22 m × 2.44 m); Owens Corning, Toledo, OH, U.S.A.). The floor of the arena was covered in brown paper. At each end of the arena, there was a square (15 × 15 cm), acoustically transparent cutout in the arena wall. A Bose Soundlink Color 2 (Bose Corporation) speaker was placed adjacent to each of these cutouts. Playback of the trial stimulus was calibrated to a maximum sound pressure level of 75 dB (re. 20 μPa, fast RMS, C-weighted) measured 1 m from the playback speaker using an Extech SDL600 sound level meter.

To control for side bias, we randomized which end of the arena was used for playback between subjects. Each female completed three phonotaxis trials, one with each of the acoustic stimuli (27%, 60% and 72% long chirp); we randomized trial order for each subject. Each female completed only one behavioural test each day to control for effects of recent experience on female behaviour. Trials were carried out during the scotoperiod, when crickets are most active. Prior to behavioural testing, each female was transferred to a clean plastic cup and placed in a darkened room. At the beginning of each trial, the subject was placed 1 m from the playback speaker and restrained under the plastic cup. To minimize any effects of chemical signals left on the arena floor, each subject was placed on a clean piece of paper. Each trial began with 1 min of acclimation to the arena in quiet, under red light, and then playback began. Following 30 s of playback, the cup was lifted to release the subject into the arena. Trials were scored in real time by an observer who recorded whether or not the female responded by making antennal contact with the speaker. If the subject did respond, we recorded the response latency as the time elapsed between release from the cup and making antennal contact with the speaker. Both the probability of approaching a playback speaker and the latency to respond to song are commonly used measures of female preferences in crickets and other phonotactic animals (Bailey, 2008; Lierheimer & Tinghitella, 2017; Tanner, Garbe et al., 2019; Tanner et al., 2017; Wagner, 1998). Receivers approach speakers broadcasting attractive songs more often and more quickly than they approach speakers broadcasting unattractive songs.

Analysis

Statistical analyses were carried out in R v.4.0.4 (R Core Team, 2021) using generalized estimating equations (GEE), which are designed for repeated measures of the same individual and compatible with both binary and continuous response variables (Hardin & Hilbe, 2012). We first fitted a pair of GEE models to examine the effect of the population of subjects on their probability of making speaker contact and their latency to respond. Because we found qualitative differences in female preferences across populations, as well as population differences in response latencies, we treated each population separately in further analyses. For each population, one model examined the probability of responding by making antennal contact with the speaker (Kaua'i: $N_{\text{subjects}} = 105$, $N_{\text{trials}} = 278$; O'ahu: $N_{\text{subjects}} = 108$, $N_{\text{trials}} = 303$; Hilo: $N_{\text{subjects}} = 115$, $N_{\text{trials}} = 310$) and the second model examined the latency to respond for the subset of tests in which the subject made antennal contact with the speaker (Kaua'i: $N_{\text{subjects}} = 97$, $N_{\text{trials}} = 224$; O'ahu: $N_{\text{subjects}} = 106$, $N_{\text{trials}} = 266$; Hilo: $N_{\text{subjects}} = 112$, $N_{\text{trials}} = 262$). Each model included the acoustic treatment, the test stimulus and their two-way interaction as predictor variables. All models were fitted with exchangeable correlation structures, which assume that observations of the same individual are equally correlated.

RESULTS

Populations did not differ significantly in the overall probability of responding to playback by contacting the speaker. On average, subjects contacted the speaker with a probability of 0.806 in the Kaua'i population, 0.878 in the O'ahu population and 0.845 in the Hilo population (Fig. 2a). However, populations differed in their latency to respond (mean ± SD), with females from O'ahu responding significantly faster (60.6 ± 47.6 s) than the reference population of Hilo (81.2 ± 59.5 s; $\beta = -21.67$, $W = 14.7$, $P < 0.001$; Fig. 2b), while Kaua'i females responded as quickly (91.2 ± 62.0 s) as Hilo females ($\beta = 9.86$, $W = 2.2$, $P = 0.138$). Because subjects from the three populations behaved differently, we treated them separately in all further analyses.

In the Hilo population (where most wild males can sing), subjects were significantly more likely to respond to playback of the 60% long chirp song ($\beta = 0.154$, $W = 4.11$, $P = 0.043$; Fig. 3a, Table 1) than to the 27% long chirp stimulus that served as the reference condition. There were no significant effects of acoustic treatment, indicating that female preferences were not altered by their experience of song quality during development. Response latency was unaffected by either the trial stimulus or the acoustic experience treatment (Table 1).

In the O'ahu population (where about half of wild males can sing), there were no significant effects of trial stimulus on the probability of making contact with the playback speaker, indicating no consistent peak preference that persisted irrespective of acoustic treatment. Females that experienced 72% long chirp during the acoustic treatment phase were more likely overall to respond to playback by making antennal contact with the speaker ($\beta = 0.180$, $W = 5.59$, $P = 0.018$) than females that experienced 27% (population average) long chirp (Fig. 3c, Table 1). Females that experienced 60% long chirp during the acoustic treatment phase were also marginally, but not significantly, more likely to respond to playback ($\beta = 0.152$, $W = 3.44$, $P = 0.064$; Table 1). Treatment*stimulus interaction effects showed that O'ahu females exposed to the 72% acoustic treatment became more selective, responding significantly faster to both the 60% ($\beta = -22.7$, $W = 3.95$, $P = 0.047$) and 72% long chirp songs ($\beta = -31.29$, $W = 4.22$, $P = 0.040$; Fig. 3d).

In the Kaua'i population (where very few wild males can sing), females showed no preference with regard to the quality of the playback stimulus and no plasticity in their selectivity. Neither trial stimulus nor acoustic treatment significantly affected either the probability of responding to playback or response latency (Table 1, Fig. 3).

DISCUSSION

Our data provide some support for the hypothesis that female mating behaviour is plastic and mediated by experience of signal quality. However, the plastic effects were only observed in the O'ahu population, and the predictions of the mating assurance in a variable environment hypothesis were not uniformly upheld. O'ahu was the only population in which we found significant acoustic treatment effects. We expected peak preferences that persisted across acoustic treatments. Where plasticity in female preferences was evident, we expected that females raised in the presence of preferred signals would be more selective than females raised in the absence of such signals, but our results did not follow this pattern. Rather, O'ahu females raised hearing songs with a high percentage of long chirp became generally more responsive and responded more quickly to attractive songs. Our results point to limited song quality-mediated plasticity in female mating behaviour.

We predicted population differences in our experimental results in part because the island populations in the Hawaiian Archipelago seem to differ in the conditions that are expected to select for plasticity. We expected conditions in our study population on O'ahu to favour plasticity more than the other two populations, because about half of males are flatwings in that population (Pascoal et al., 2014; Zuk et al., 2018). We thought this might lead to spatial heterogeneity in cues about the availability of singing males because songs degrade quickly as a result of geometric spreading (Simmons, 1988), and that this could lead to a highly variable environment with respect to the costs and benefits of expressing preferences for song quality (Jennions & Petrie, 1997). In this framework, the quality of song heard during development would be a reliable cue about the availability of high-quality mates upon reaching adulthood and female phenotypes might experience variable success across environments: selective females should benefit when high-quality mates are readily available, while permissive females should benefit when preferred mates are rare or absent. Consistent with these ideas, O'ahu (where around half of males can sing) was the only population in which we observed an effect of the acoustic experience treatment. Because Hawaiian *T. oceanicus* females prefer above-average percentages of long chirp (Bailey et al., 2008),

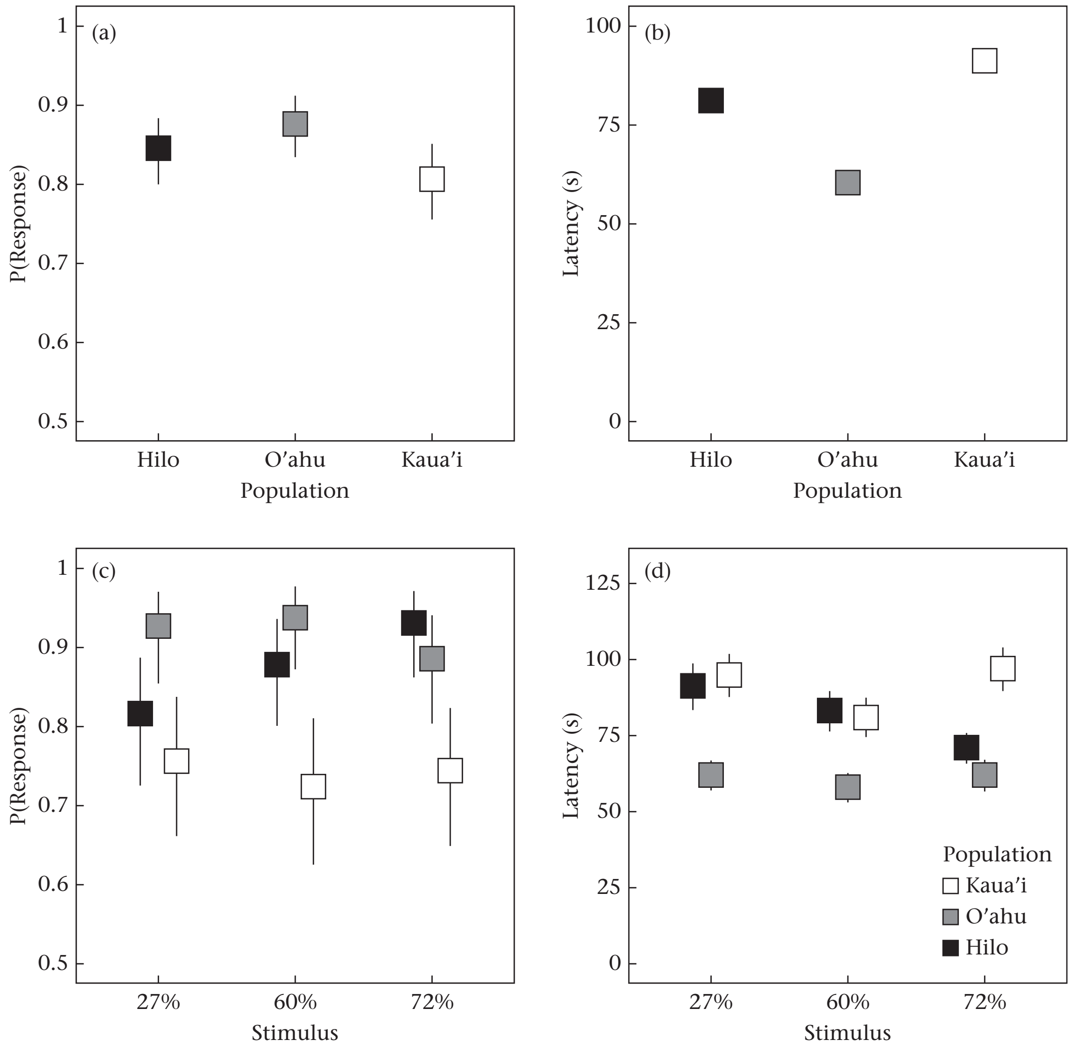

Figure 2. Population differences in phonotactic responses: (a) the overall probability of response by population, (b) the response latency by population, (c) the probability of response by population and trial stimulus and (d) the latency to respond by population and trial stimulus. Response latencies are calculated for the subset of subjects that responded by playback. Symbols depict group means. Error bars show 95% Clopper–Pearson ('exact binomial') confidence intervals in panels (a) and (c) and standard errors in panels (b) and (d).

females reared with a high percentage of long chirp songs may be more likely to respond to song because their acoustic cues indicate that all available singers are of relatively high quality. Female preferences for long chirp were not significantly affected by acoustic experience in either the Hilo population (where almost all males can sing) or the Kaua‘i population (where almost no males can sing), which is consistent with the idea that a more variable environment selects for plasticity, while a less variable environment does not.

Within populations, the mating assurance in a variable environment hypothesis (Fowler-Finn & Rodríguez, 2011) made two predictions. First, that peak mating preferences should remain unchanged across environments. Second, that females should be more selective when reared in the presence of higher-quality songs and less selective when reared in the presence of lower-quality songs. Changes in female selectivity across treatments would be indicated by significant interaction effects between acoustic treatment and acoustic stimulus. In the O‘ahu population, we found support for only the second prediction. Females exposed to the highest proportions of long chirp during the acoustic treatment phase responded more quickly to high-quality (60% and 72% long chirp) songs compared to average (27% long chirp) songs. In other words, receivers were more selective when they experienced high-quality signals during development. However, we did not observe a significant main effect of trial stimulus; that is, there was no clear peak preference in the O‘ahu population that persisted irrespective of the experience of songs during development. Data did not support an alternative, environment-matching hypothesis, in which females might prefer the familiar phenotype from the acoustic experience phase (Hebets, 2003; Westerman et al., 2014), or a novelty-preference hypothesis, in which females might prefer an unfamiliar phenotype (Daniel et al., 2019; Royle et al., 2008).

Indeed, among the most striking results were the high level of variation within and between populations and the observation that, for the most part, females did not seem to adjust their behaviour to suit their rearing environment as expected. The among-population variation in female preferences we found is consistent with other studies that have shown geographical variation in female preference functions (Simmons et al., 2001). In combination with other findings showing that female reproductive behaviours are affected by the presence or absence of song (Bailey & Zuk, 2008; Balenger & Zuk, 2015; Heinen-Kay et al., 2019; Lierheimer & Tinghitella, 2017; Swanger & Zuk, 2015), our data point to limited plasticity in female behaviours. Despite the many fitness benefits of plasticity documented in diverse taxa, phenotypes are not infinitely plastic because plasticity has inherent costs and limits, including those

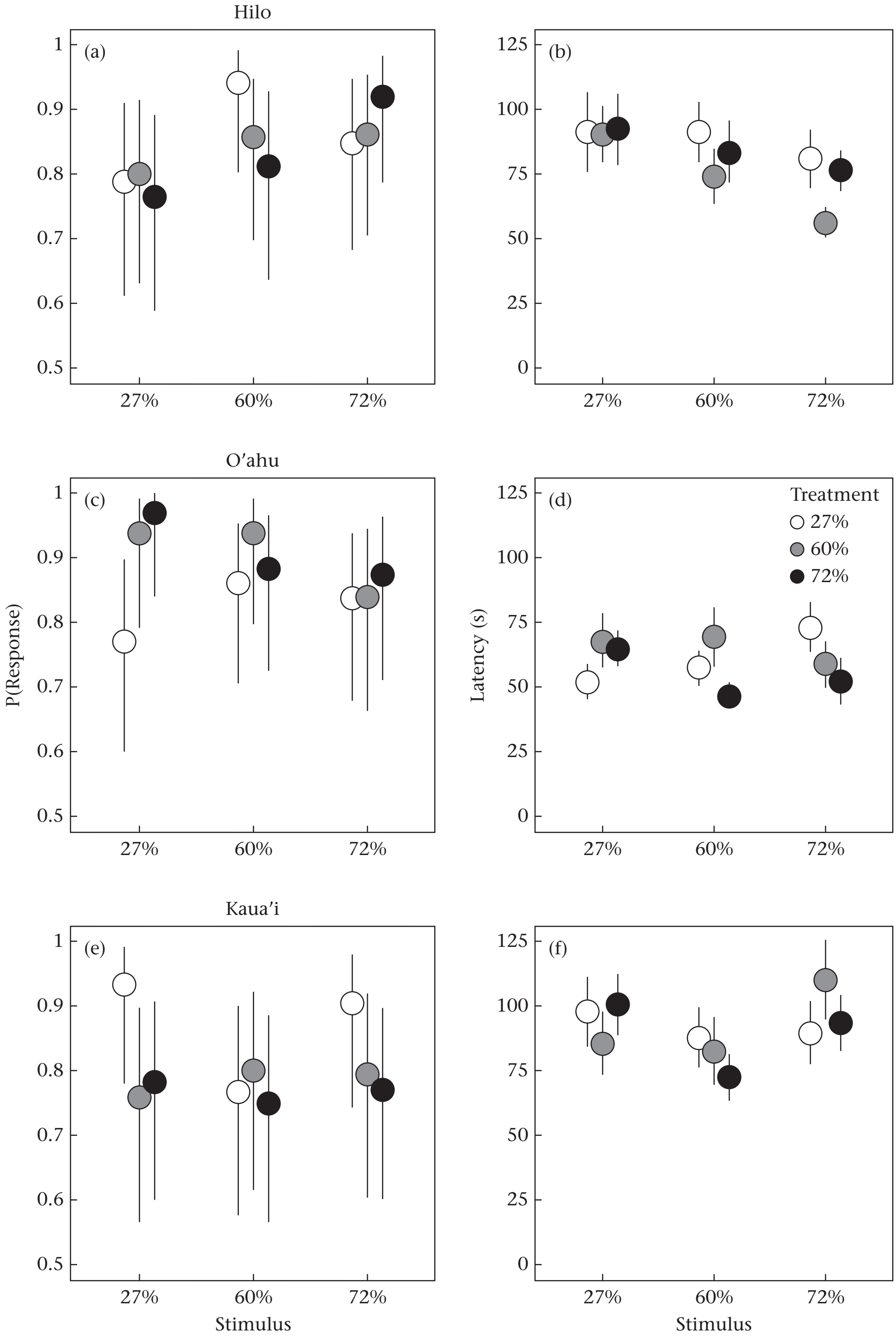

Figure 3. Treatment and stimulus effects for the three study populations: (a, d) Hilo, (b, e) O'ahu and (c, f) Kaua'i. The plots in the left-hand column show the probability of responding to stimulus playback, while the plots in the right-hand column show the latency to respond to playback calculated for the subset of subjects that responded. Symbols depict group means. Error bars in panels (a, c, e) show 95% Clopper–Pearson ('exact binomial') confidence intervals, while error bars in panels (b, d, f) show standard errors.

related to information acquisition and reliability (DeWitt et al., 1998; Murren et al., 2015; Snell-Rood et al., 2010). Even if selection favoured song quality-mediated plasticity in female mating preferences in Hawaiian *T. oceanicus*, a response to selection is not guaranteed for multiple possible reasons, including limited underlying standing genetic variation.

Female *T. oceanicus* generally have pronounced and genetically based, open-ended preference functions for the percentage of long chirp (Hoy, 1974; Hoy et al., 1977; Simmons, 2004; Tanner & Simmons, in press), but there is also geographical variation in female preference functions (Simmons et al., 2001). Hawaiian females have, in the past, shown a peak preference for 60% long chirp

Table 1
Output from generalized estimating equations models examining the probability of responding to playback and latency to respond

Population	Response variable	Effect	Estimate	SE	*W*	*P*
Hilo	**P(Response)**	**Intercept**	**0.791**	**0.07**	**124.22**	**<0.001**
		Treatment 60%	0.014	0.10	0.02	0.888
		Treatment 72%	−0.023	0.10	0.05	0.825
		Stimulus 60%	**0.154**	**0.08**	**4.11**	**0.043**
		Stimulus 72%	0.056	0.08	0.45	0.503
		Treatment 60%∗stimulus 60%	−0.101	0.10	0.93	0.334
		Treatment 72%∗stimulus 60%	0.102	0.12	0.69	0.406
		Treatment 60%∗stimulus 72%	0.005	0.12	0.00	0.968
		Treatment 72%∗stimulus 72%	0.098	0.12	0.62	0.430
	Latency	**Intercept**	**96.692**	**14.85**	**42.42**	**<0.001**
		Treatment 60%	−4.686	18.21	0.07	0.800
		Treatment 72%	0.266	19.93	0.00	0.990
		Stimulus 60%	−1.977	13.69	0.02	0.890
		Stimulus 72%	−12.301	17.64	0.49	0.490
		Treatment 60%∗stimulus 60%	−15.585	17.00	0.84	0.360
		Treatment 72%∗stimulus 60%	−12.243	21.00	0.34	0.560
		Treatment 60%∗stimulus 72%	−22.314	20.45	1.19	0.280
		Treatment 72%∗stimulus 72%	−7.956	21.30	0.14	0.710
O'ahu	**P(Response)**	**Intercept**	**0.781**	**0.07**	**126.73**	**<0.001**
		Treatment 60%	0.152	0.08	3.44	0.064
		Treatment 72%	**0.180**	**0.08**	**5.59**	**0.018**
		Stimulus 60%	0.090	0.08	1.42	0.233
		Stimulus 72%	0.063	0.06	1.24	0.266
		Treatment 60%∗stimulus 60%	−0.081	0.10	0.67	0.412
		Treatment 72%∗stimulus 60%	−0.169	0.10	2.82	0.093
		Treatment 60%∗stimulus 72%	−0.154	0.09	3.06	0.080
		Treatment 72%∗stimulus 72%	−0.139	0.08	2.85	0.092
	Latency	**Intercept**	**53.440**	**6.87**	**60.46**	**<0.001**
		Treatment 60%	13.730	12.43	1.22	0.269
		Treatment 72%	11.890	9.93	1.43	0.231
		Stimulus 60%	5.050	8.70	0.34	0.561
		Stimulus 72%	19.290	11.38	2.87	0.090
		Treatment 60%∗stimulus 60%	−2.170	15.40	0.02	0.888
		Treatment 72%∗stimulus 60%	**−22.770**	**11.45**	**3.95**	**0.047**
		Treatment 60%∗stimulus 72%	−27.840	18.40	2.29	0.130
		Treatment 72%∗stimulus 72%	**−31.290**	**15.24**	**4.22**	**0.040**
Kaua'i	**P(Response)**	**Intercept**	**2.551**	**0.69**	**13.81**	**<0.001**
		Treatment 60%	−1.377	0.81	2.86	0.091
		Treatment 72%	−1.295	0.80	2.60	0.107
		Stimulus 60%	−1.341	0.73	3.42	0.065
		Stimulus 72%	−0.392	0.95	0.17	0.680
		Treatment 60%∗stimulus 60%	1.532	0.86	3.21	0.073
		Treatment 72%∗stimulus 60%	1.075	0.81	1.75	0.185
		Treatment 60%∗stimulus 72%	0.594	1.13	0.28	0.600
		Treatment 72%∗stimulus 72%	0.313	1.08	0.08	0.772
	Latency	**Intercept**	**102.992**	**13.24**	**60.50**	**<0.001**
		Treatment 60%	−13.377	17.81	0.56	0.453
		Treatment 72%	−0.277	17.62	0.00	0.987
		Stimulus 60%	−11.511	15.54	0.55	0.459
		Stimulus 72%	−13.403	12.63	1.13	0.289
		Treatment 60%∗stimulus 60%	4.585	23.13	0.04	0.843
		Treatment 72%∗stimulus 60%	−12.761	20.02	0.41	0.524
		Treatment 60%∗stimulus 72%	33.647	19.45	2.99	0.084
		Treatment 72%∗stimulus 72%	1.893	19.74	0.01	0.924

Hilo ($N_{\text{subjects}} = 115$), O'ahu ($N_{\text{subjects}} = 108$) and Kaua'i ($N_{\text{subjects}} = 105$) populations were treated separately. All models were fitted with exchangeable correlation structures. Model terms significant at an $\alpha = 0.05$ level are shown in bold.

(Bailey & Zuk, 2008). It was therefore unexpected that we found no consistent peak preferences for a longer long chirp (i.e. stimulus effects) in the O'ahu and Kaua'i populations, while Hilo females preferred the 60% long chirp songs. We speculate that both recent selection and drift may have affected this rapidly evolving signalling system since the observation of long chirp preferences documented by Bailey and Zuk (2008). Hawaiian populations have been affected by the invasion of the flatwing mutations (which render males obligately silent) to different extents and flatwing frequencies are also highly variable in both time and space (Pascoal et al., 2014; Zuk et al., 2018). Furthermore, in addition to the flatwing phenotype, several other novel phenotypes (including 'purring', 'small-wing' and 'curlywing') that mitigate the risk of parasitization by modifying or reducing the wing structures males use to sing have recently been discovered in the Hawaiian islands (Rayner et al., 2019; Tinghitella et al., 2018). Given the dynamic state of this signalling system and the general trend towards song reduction and loss, female-mediated selection on male song quality may have become relaxed while selection on males' ability to produce any audible song at all took precedence (Tanner, Swanger et al., 2019). Further research is needed to determine whether and how precopulatory sexual selection acts on song characteristics since the appearance of these novel phenotypes that modify or prevent song.

It is also possible that we did not find clear support for the mating assurance in a variable environment hypothesis because we expected peak female preference to be above the population's mean long chirp value (directional sexual selection) and designed our experiment to focus on population average percentages of long chirp and above. We know that females prefer not to approach songs with low percentages of long chirp or songs that completely lack a long chirp segment (Bailey & Zuk, 2008; Lierheimer & Tinghitella, 2017). Because the present experiment excluded such stimuli, we likely tested a range of stimuli that female *T. oceanicus* find generally acceptable, which may have led to limited ability to detect strong female preferences. We might have observed different effects if our design had also covered the below-average end of the distribution of male phenotypes. However, a recent study of *T. oceanicus* from Kaua'i manipulated the quantity and quality of song in the acoustic environment (Lierheimer & Tinghitella, 2017). In that study, some females were exposed to a 60% long chirp stimulus similar to the one used in our study, while other females experienced songs that entirely lacked a long chirp segment (0% long chirp), a trait value well below the minimum percentage of long chirp tested here (Lierheimer & Tinghitella, 2017). That study reported an effect of the presence versus absence of song on female mating behaviours, but found no effect of song quality (the percentage of long chirp; Lierheimer & Tinghitella, 2017). Those findings corroborate our own results from the Kaua'i population.

The presence versus absence of song in the acoustic environment mediates plasticity in multiple aspects of *T. oceanicus* mating behaviour and reproductive physiology, including female investment in eggs and ovarioles (Heinen-Kay et al., 2019), female responsiveness to song (Bailey & Zuk, 2008; Swanger & Zuk, 2015), male investment in sperm competitive traits (Moschilla et al., 2020; Simmons & Lovegrove, 2017) and male mate searching behaviour (Balenger & Zuk, 2015). In some other insects, female behaviour is sometimes mediated not only by the presence of signalling, but also by its quality (Fowler-Finn & Rodríguez, 2011; Rebar et al., 2019), but we found mixed support for the idea that plasticity in female mating behaviour is mediated by song quality in Hawaiian *T. oceanicus*. We conclude that the quality of song in the acoustic environment is a much less important cue for the development of female mating preferences than the presence versus absence of song. While we manipulated only one aspect of signal quality, we note that acoustic signals are multivariate phenotypes upon which females impose multivariate selection (Bentsen et al., 2006; Tanner et al., 2017). It may be that the percentage of long chirp is not the single most important signal feature females could use to evaluate the presence of high-quality males in their environment, or that they use multiple traits to evaluate their prospects. Future work should continue to investigate whether or not cricket behaviour and reproductive physiology is mediated by acoustic cues of mate quality in addition to the presence versus absence of mates.

Author Contributions

J.C.T. and M.Z.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing – review and editing. **J.C.T. and E.R.J.:** Data curation, investigation. **J.C.T.:** writing – original draft.

Declaration of Interest

None.

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