



Original Article

Spoiled for choice: number of signalers constrains mate choice based on acoustic signals

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INTRODUCTION

Across animal taxa, communication mediates social interactions with important fitness consequences, including mate attraction and courtship (Bradbury and Vehrencamp 1998; Gerhardt and Huber 2002; Maynard Smith and Harper 2003; Rosenthal 2017). Signalers (typically males) display to attract prospective mates and receivers (typically females) use signals to make mating decisions and thereby gain fitness benefits for themselves and their offspring (Andersson 1994; Hasselquist et al. 1996; Welch et al. 1998; Møller and Alatalo 1999; Andersson and Simmons 2006). More than a century of research has investigated the communication behaviors involved in mate choice and sought, in particular, to measure female preference functions, which describe the strength of female responses to a range of trait values (Andersson 1994; Rosenthal 2017). Some acoustically communicating animals, such as orthopteran insects and anuran amphibians, have proved excellent models for research on receiver behavior because receivers exhibit phonotaxis (movement toward sounds they recognize as conspecific signals) and respond readily and unequivocally to audio playback

of synthetic sounds (Gerhardt and Huber 2002). Phonotaxis assays are regularly used to measure the strength of sexual selection on acoustic signals and answer other biological questions, including about trait elaboration, reproductive isolation, population divergence, and speciation (Brooks et al. 2005; Podos 2010; Akre et al. 2011; Pfennig and Rice 2014).

Many animals communicate in physically and socially complex environments, where noise from multiple biotic, abiotic, and anthropogenic sources may impede communication (Brumm and Slabbekoorn 2005; Römer 2013; Reichert and Ronacher 2015; Wiley 2015; Templeton et al. 2016; Bent et al. 2018; Coss et al. 2020; Dominoni et al. 2020; Römer 2020; Bent et al. 2021). However, noise is often excluded from laboratory studies of animal behavior and, when it is examined specifically, noise is typically investigated using playback of masking stimuli. Crucially, “noise” is broadly defined as any factor that impairs signal detection or discrimination (Shannon 1948; Brumm and Slabbekoorn 2005; Wiley 2015), and as such, noise need not necessarily be acoustic or itself devoid of information. Something that functions as a signal in one context can be noise in another context.

Among acoustically communicating animals, the sound produced by an aggregation of signalers, or “chorus”, is a well-known

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source of noise (Schwartz et al. 2001; Wollerman and Wiley 2002; Bee et al. 2012; Römer 2013; Schmidt and Balakrishnan 2015; Tanner and Bee 2019; Tanner and Bee 2020a). Choruses may form because individual signalers gravitate to areas rich with the resources needed by receivers or their offspring (Thornhill and Alcock 1983; Gerhardt and Huber 2002). In lek-based mating systems, males gather to display and females choose among potential sires for their offspring but gain no other material benefits (Höglund and Altalo 1995). Regardless of the ultimate reason for chorus formation, individuals gathered in such aggregations must compete with one another to be heard. In some species, this competition constitutes defense of short- or long-term calling sites or territories, and the resulting spatial separation of signalers may minimize masking interference by competitors (Evans 1983; Schmidt and Römer 2011; Römer 2013). In others, fine-scale patterns of signal timing among conspecifics reveal individual strategies for avoiding the acoustic interference caused by neighbors that are signaling simultaneously (Zelick and Narins 1985; Schwartz 1993). Alternatively, some insects strategically “jam” the signals of competitors by signaling at the same time (Greenfield and Roizen 1993; Greenfield 1994; Legendre et al. 2012). Even in the absence of strategies for either avoiding or causing acoustic interference, when signals produced by competing males are timed randomly with respect to one another, noise is an inevitable outcome of individual signalers competing for acoustically mediated mating opportunities. This noise can limit the opportunity for, or increase the cost of, female mate choice based on acoustic signals (Wollerman 1999; Wollerman and Wiley 2002; Schmidt and Balakrishnan 2015; Wiley 2015).

Given that a chorus is an emergent property of individual signalers producing signals, how many signals does it take to generate the noise that impairs signal detection and discrimination? We used the Australian field cricket *Teleogryllus oceanicus* to explore this problem. As in other gryllid crickets, *T. oceanicus* males produce a long-distance calling song by stridulation that functions to attract female conspecifics (Huber et al. 1989). The species has long been a productive model for exploring the neuroethology and behavioral ecology of acoustic signaling (Cade 1975; Doolan and Pollack 1985; Pollack 1986; Huber et al. 1989; Balakrishnan and Pollack 1996; Bailey and Haythornthwaite 1998; Zuk et al. 1998; Simmons et al. 2001). In nature, individual signalers are nonrandomly distributed in space, forming “clumps” with the nearest neighbor sometimes as close as 0.9 m away (Cade 1981; Campbell 1990). As a result, a *T. oceanicus* chorus can be relatively densely populated and generate high-amplitude chorus noise. Whether and how the aggregate of signals produced by individual males that make up a chorus impairs signal detection and discrimination by receivers is important to our understanding of the strength of sexual selection acting in natural populations.

Here, we present results from three experiments designed to understand how receiver preferences are expressed in scenarios with multiple signalers. First, we assayed female preferences for the number of pulses in the long chirp portion of the calling song (Figure 1). This song trait has been shown previously to be under sexual selection in *T. oceanicus*, with receivers showing a population-level preference for higher numbers of long chirp pulses (Simmons et al. 2001). Second, having confirmed the female preference for more long chirp pulses, we gave receivers a series of behavioral tasks

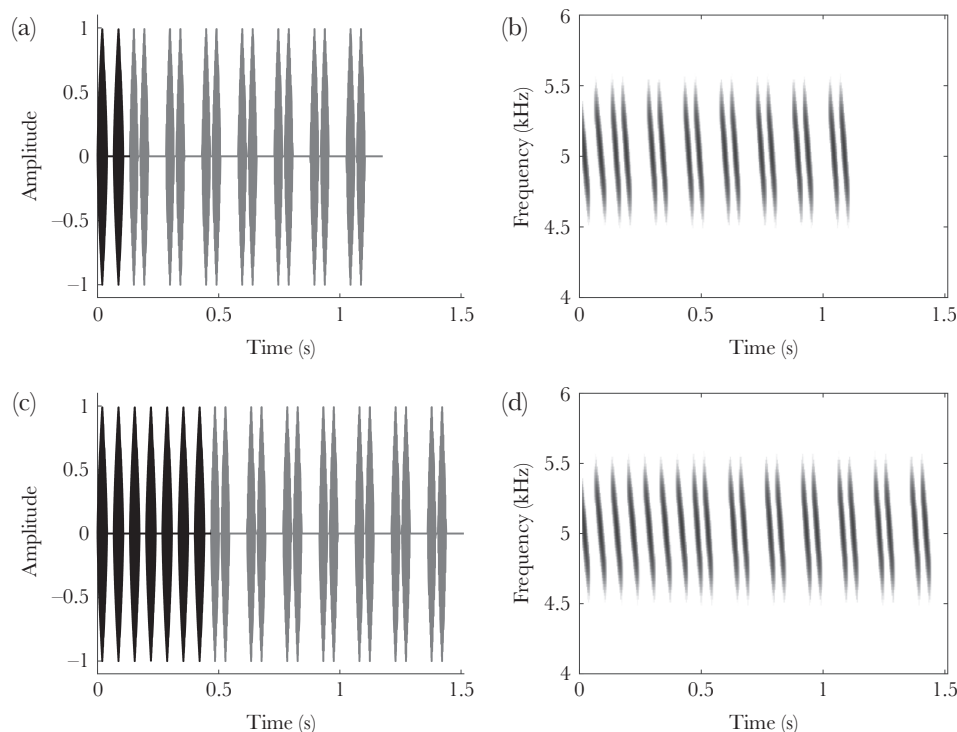


Figure 1

Synthetic *Teleogryllus oceanicus* songs used as stimuli. The song consists of two parts called the long chirp (black portions of waveforms in a and c) and the short chirps (the gray portions of waveforms in a and c). The alternative stimuli had either two (top panels) or seven (bottom panels) long chirp pulses. Both stimuli had seven short chirps. Each sound pulse consisted of a frequency-modulated downsweep with a bandwidth of 749 Hz and a center frequency of 5031 Hz (b, d).

in which they discriminated between the preferred stimulus and either one, three, five, or seven presentations of the nonpreferred stimulus. We hypothesized that a relatively small number of songs was sufficient to create the emergent masking effect of chorus noise. If so, we predicted that, as the number of stimuli increased, receivers would be less likely to respond phonotactically to playback of song stimuli and that receivers that did respond would be less likely to approach the speaker broadcasting the preferred stimulus. Finally, we conducted an experiment to determine whether our results were attributable to the increasing number of stimuli in multi-choice scenarios, or an artifact of the decreasing angular separation of playback speakers.

METHODS

Insects are not subject to ethical review in Australia, but all procedures described here met with the standards of the Animal Behavior Society/Association for the Study of Animal Behaviour Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

Subjects and rearing

Subjects were female *T. oceanicus* from an outbred laboratory colony descended from a population located in Carnarvon, Western Australia. Crickets were housed in a constant temperature room at 26°C with a photo-reversed 12:12 light cycle. Because female phonotaxis behavior is altered by growing up in the absence of song (Bailey and Zuk 2008; Swanger and Zuk 2015; Lierheimer and Tinghitella 2017), we ensured that our subjects were exposed to the song of live, adult male conspecifics throughout their development. Phonotaxis behavior in field crickets is sensitive to the age and mating status of individuals (Judge et al. 2010; Moschilla et al. 2018; Tanner et al. 2019). Females usually become phonotactic prior to the sixth day after eclosion (Loher et al. 1993). To limit the effect of age on female behavior, we restricted the age window for behavioral testing to 10–13 days after eclosion by checking isolated individuals daily and noting the date of final adult eclosion. Female responsiveness to male song increases with age past 14 days (Moschilla et al. 2019) so we likely tested crickets during their peak period of selectivity. To control for the effect of mating on female behavior, we ensured all subjects remained unmated by isolating females from the colony as late-stage juveniles, when they could be unambiguously sexed but were not yet sexually mature. Subjects were housed individually in plastic cups with lids and given *ad libitum* access to dry cat food and water-soaked cotton.

Experimental design overview

We first assessed female preferences for the number of long chirp pulses in the song (Figure 1) using a phonotaxis experiment in which subjects ($n = 20$) chose between a 7-pulse and 2-pulse stimulus. The format of this preliminary experiment was a two-alternative forced-choice test, in which subjects were required to choose one of the two speakers separated by 180° (all other details about the test arena, protocol, and equipment were identical to procedures in the multi-choice and angular separation experiments, as described in detail below). Subjects that did not respond in this forced-choice test were retested the following day and, in the event that they did not respond to playback a second time, were not tested further ($n = 2$ of 20). In our preliminary assessment of female preferences, 14 of 18 females that responded phonotactically approached the speaker broadcasting the 7-pulse stimulus (binomial test, $H_A: \theta \neq$

0.5; $P = 0.03$; 95% CI = [0.524, 0.936]; Figure 2). We, therefore, considered the 7-pulse stimulus to be the “preferred” stimulus and the 2-pulse stimulus to be the “nonpreferred” stimulus.

We then conducted the multi-choice experiment, in which we gave an independent sample of subjects ($n = 97$) a series of four phonotaxis tests in which one speaker played the preferred, 7-pulse stimulus while one, three, five, or seven other speakers played the nonpreferred, 2-pulse stimulus. Subjects were assigned to blocks that corresponded to a single day of behavioral testing. For each block, we randomized the order in which the tests were presented and the speaker assignment for the 7-pulse stimulus for each test. Twenty of 97 individuals failed to respond in any test, and were excluded from the analysis. 74 individuals completed all four tests, one individual completed three tests, one individual completed two tests, and one individual completed one test, yielding a dataset of 304 tests of 77 individuals.

In the multi-choice experiment, the angular separation of any two speakers decreased as the number of speakers increased. We designed the angular separation experiment to test the possibility that female responses were affected by the angular separation of adjacent stimuli, rather than by the number of signalers *per se*. We gave an independent sample of subjects ($n = 56$) a series of four, two-choice phonotaxis tests in which one speaker played the preferred, 7-pulse stimulus while the other speaker played the nonpreferred, 2-pulse stimulus. Speakers were separated by either 180, 90, 60, or 45 degrees to mirror the angular separations in the 2, 4, 6, and 8-choice tests, respectively. As in the multi-choice experiment, subjects were assigned to blocks that corresponded to a single day of behavioral testing and for each block, we randomized the order of test presentation and the speaker assignment of the preferred stimulus for each test. We also replicated the experiment on each of two sides of the testing arena to preclude the possibility of side bias influencing our conclusions. Three of 56 individuals failed to respond in any test and were excluded from the analysis. The remaining 53 individuals completed all four tests, yielding a dataset of 212 tests for the angular separation experiment.

Test protocol

We assayed female behavior during the scotoperiod, when crickets are most active. Trials were carried out under red light in a square, short-walled arena (2.5 m length $\times$ 2.5 m width $\times$ 0.25 m height) constructed from interlocking foam mats (black, 0.5 m $\times$ 0.5 m;

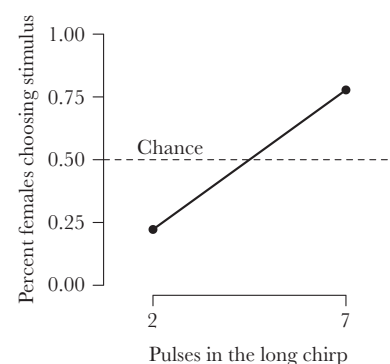


Figure 2

Directional female preference for a higher number of long chirp pulses from a two-alternative forced choice test. Fourteen of 18 receivers that responded preferred the 7-pulse signal over the 2-pulse signal.

Bunnings Group Ltd, Australia) placed on the floor of a semi-anechoic room (4.7 m length $\times$ 4.7 m width $\times$ 2.4 m height). Tests were carried out at a controlled temperature of 26°C because receiver preferences are temperature-dependent in gryllid crickets (Huber et al. 1989; Pires and Hoy 1992; Gerhardt and Huber 2002). Speakers were arranged on the floor of the arena along the circumference of a 1 m radius circle, such that all speakers were a distance of 1 m from the subject at the beginning of the trial. In the multi-choice experiment, speakers were evenly spaced around the circle in all test conditions, such that the angular separation of speakers was 180°, 90°, 60°, and 45° in the 2, 4, 6, and 8-choice tests, respectively (Figure 3a–d). The angular separation experiment presented the same speaker configurations in a series of tests with only two choices (Figure 3e–h).

At the beginning of each trial, the subject was placed at the center of the circle with a piece of egg carton large enough to hide under and covered by an acoustically transparent barrier. The subject was allowed to acclimate to the arena for two minutes. At the end of the acclimation period, playback of the acoustic stimuli began.

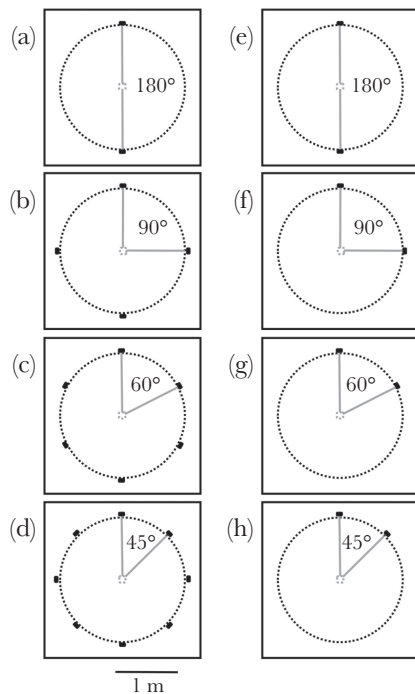


Figure 3

Diagram of speaker configurations in the multi-choice experiment (left column) and angular separation experiment (right column). Speaker arrangements in the two-choice (a), four-choice (b), six-choice (c), and eight-choice (d) tests corresponded to 180° (e), 90° (f), 60° (g), and 45° (h) in the two-choice experiments that made up the angular separation experiment. In all panels, the solid black square represents the arena wall. The dotted black circle shows the 1-meter radius that separates the subject's starting position (dotted grey circle) from each speaker; this line was not demarcated by any physical barrier within the arena. Rounded black rectangles represent speakers. The dashed, rounded rectangle at the center of each diagram represents the release point, where subjects began each test. Degree measurement annotations show the angular separation of a speaker and its nearest simulated neighbor in each condition.

Thirty seconds after the beginning of playback, the barrier was lifted by the observer by means of a pole with an attached hook so that the cricket was able to move throughout the arena. A trial ended when one of the following conditions was met: 1) the subject responded to a song stimulus by approaching a broadcasting speaker within one body length; 2) at the end of 10 min, if the subject was not walking when time expired. In the relatively rare event that a cricket was still walking at the end of 10 min, she was given one additional minute to complete the trial. Occasionally, a subject escaped the arena by jumping, flying, or climbing over the wall; in that case, the subject was given the same trial again after a timeout. When a subject escaped the arena in two consecutive tests, she was not tested further; however, tests she had already completed were included in the statistical analysis ($n = 3$ of 77 individuals in the multi-choice experiment). Females were returned to their individual cups for a timeout of at least 10 min and up to an hour between trials.

Stimuli and playback

The acoustic stimuli were synthetic *T. oceanicus* songs generated *de novo* using the SynSing graphical user interface (Tanner et al. 2020) running in MATLAB 2018b (The Mathworks, Natick, MA). The songs differed primarily in the number of pulses in the long chirp (Figure 1), which was set at either 2 or 7 pulses to approximate the minimum and maximum temperature-corrected (Platz and Forester 1988) values observed in the recordings of 168 wild males made near Cairns, Queensland, Australia (Simmons 2004). Temporal properties of male calling songs do not differ between Cairns, where the songs informing our stimuli were recorded, and Carnarvon, the source population of our subjects (Simmons et al. 2001). The total song duration was allowed to vary to accommodate the changing number of pulses. Female *T. oceanicus* show population-level preferences for more pulses in the long chirp, irrespective of total song duration (Pollack 1982; Simmons et al. 2001).

All characteristics not under manipulation were set at the population mean. Sound pulses had a center frequency of 5031 Hz and a frequency-modulated downsweep of 749 Hz. Long chirp pulses were 39 ms in duration with 28 ms interpulse intervals. The amplitude envelopes of the long chirp pulses were symmetrical and nonlinear in shape, with rise- and fall-times of 19.5 ms. Long chirp pulses reached 50% of their maximum amplitude at 35% of the rise-time and 65% of the fall-time.

The second part of the song is a series of “short chirps” that each comprise two sound pulses arranged in a couplet (Figure 1). Both song variants included 7 short chirps per song. Within the short chirp, sound pulses were 32 ms in duration with 11 ms interpulse intervals. Short chirps were separated by an interchirp interval of 74 ms. The amplitude envelopes of the short chirp pulses were symmetrical and nonlinear in shape, with rise- and fall-times of 16 ms. Short chirp pulses reached 50% of their maximum amplitude at 35% of the rise-time and 65% of the fall-time.

We broadcast acoustic stimuli using Goofly mp3 players connected to JBL GO2 speakers (JBL Consumer, Los Angeles, CA) via 3.5 mm audio cables measuring 5 m in length. Prior to testing, stimuli were calibrated to a playback level of 80 dB SPL (slow RMS, C-weighted) using a Realistic sound level meter (Intertan Australia Limited, Newcastle, NSW, Australia) placed with its microphone at the location of a subject at the beginning of a trial, 1 m from the sound source.

To preclude any possible leader–follower effects, playback of all stimuli in a given trial began simultaneously. To prevent

artifacts associated with the entrainment of pulses between identical nonpreferred stimuli played from different speakers, the audio track on each playback device was advanced to a haphazard timepoint in the song period prior to the beginning of any trial. That is, in trials with more than one nonpreferred stimulus, the timing relationship between speakers broadcasting the same song was invariant for the length of that trial, but there was no systematic relationship between the relative pulse timing of stimuli played from different speakers across the experiment. Note that the preferred and nonpreferred stimuli had different song periods and so necessarily were variably timed with respect to one another over the course of any trial.

Statistical analyses

For both the multi-choice experiment and the angular separation experiment, we fit generalized estimating equations (GEE) to test for an effect of the number of stimuli (multi-choice experiment) or angular separation of speakers (angular separation experiment) on five dependent variables: the probability that a subject left the release point, the probability that a subject responded phonotactically by approaching a broadcasting speaker, the probability that a subject chose the 7-pulse stimulus, the latency to leave the release point and the latency to respond to playback. GEE is an extension of generalized linear models designed explicitly to account for repeated measures of the same individual (Hardin and Hilbe 2012). We specified exchangeable correlation structures, which assume homogenous correlations among observations of the same subject. In each model, we included the block and the subject's age, measured in days after eclosion, as covariates. In the model examining the probability of choosing the 7-pulse stimulus, we additionally included the latency to respond as a predictor. Because we fit five GEE models, we applied a Bonferroni correction to account for multiple testing within each of our two independent experiments; after correction, the significance level, α , was 0.01.

Table 1

Output from five generalized estimating equations (GEE) models examining the results of the multi-choice experiment ($n = 304$ tests of 77 receivers). Model terms that were significant after the Bonferroni correction ($\alpha = 0.01$) are shown in bold.

Response variable	Independent variable	Estimate	Standard error	Wald statistic	P
P(Left release point)	Intercept	0.421	0.358	1.38	0.240
	Block	0.018	0.005	16.06	6.10E-05
	Age	0.027	0.030	0.8	0.370
	Number of stimuli	-0.050	0.010	23.34	1.40E-06
P(Response)	Intercept	0.814	0.405	4.05	0.044
	Block	0.012	0.005	5.21	0.022
	Age	0.023	0.032	0.53	0.468
	Number of stimuli	-0.203	0.056	12.91	3.300E-04
	Number of stimuli ²	0.013	0.006	5.74	0.017
P(Chose the preferred signal)	Intercept	1.236	0.334	13.32	2.600E-04
	Block	0.005	0.006	0.62	0.433
	Age	-0.044	0.025	3.04	0.081
	Number of stimuli	-0.098	0.015	45.18	1.80E-11
	Latency to respond	2.560E-04	1.600E-04	2.56	0.110
Latency to leave release point	Intercept	306.48	155.91	3.86	0.049
	Block	-2.79	2.07	1.83	0.177
	Age	-11.17	12.5	0.8	0.371
	Number of stimuli	-1.43	4.71	0.09	0.762
Latency to respond	Intercept	362.94	179.29	4.1	0.043
	Block	-4.54	2.05	4.9	0.027
	Age	-10.35	14.47	0.51	0.474
	Number of stimuli	-2.56	5.98	0.18	0.669

In all three experiments, we used binomial tests to determine whether subjects in each test condition chose the 7-pulse stimulus more often than expected by chance. This was particularly important in the multi-choice experiment, when the probability of choosing the 7-pulse stimulus is expected to decline with increasing number of stimuli, even if subjects choose among stimuli at random. Though we were testing hypotheses compatible with the use of one-sided binomial tests, we opted to use the more conservative two-sided binomial test. In the multi-choice experiment, the Pearson product-moment correlation coefficient was used to assess the relationship between two metrics of female response, the probability of leaving the release point and the probability of responding to playback.

All analyses were carried out in R version 4.0.4 (R Core Team 2021). We used the *geepack* package to fit GEE models and the *ggplot2* package to generate some figures (Halekoh et al. 2006; Wickham 2016). Output from GEE models is provided in Table 1 (multi-choice experiment) and Table 2 (angular separation experiment).

RESULTS

Multi-choice experiment

Across the multi-choice experiment, subjects responded to playback in 183 of 304 (60.2%) tests. Of the 121 tests (58 unique receivers) in which the subject did not respond to playback, 91 (48 unique receivers) ended without the subject having left the release point. Receivers left the release point without indicating a choice in 1, 8, 10, and 11 trials in the 2-, 4-, 6-, and 8-choice tests, respectively. As the number of stimuli increased, subjects became less likely to leave the release point ($\beta = -0.050$, $W = 23.34$, $P < 0.001$; Figure 4a) and less likely to respond to playback by approaching a speaker ($\beta = -0.203$, $W = 12.91$, $P < 0.001$; Figure 4b). These two metrics of receiver response were strongly correlated, such that receivers that left the release point also responded to playback by approaching a speaker in 85.9% of trials (183 of 213 trials;

Table 2

Output from five generalized estimating equations (GEE) models examining the results of the angular separation experiment ($n = 212$ tests of 53 receivers). Model terms that were significant after the Bonferroni correction ($\alpha = 0.01$) are shown in bold.

Response variable	Independent variable	Estimate	Standard error	Wald statistic	P
P(Left release point)	Intercept	0.116	0.328	0.13	0.723
	Block	0.013	0.007	3.35	0.067
	Age	0.060	0.027	5.06	0.024
	Angular separation	0.000	0.000	0.04	0.850
P(Response)	Intercept	-0.121	0.385	0.10	0.753
	Block	0.007	0.008	0.83	0.362
	Age	0.085	0.027	9.84	0.002
	Angular separation	-0.001	0.003	0.04	0.845
P(Chose the preferred signal)	Angular separation^2	0.000	0.000	0.01	0.916
	Intercept	0.966	0.471	4.21	0.040
	Block	0.013	0.009	2.07	0.150
	Age	0.011	0.037	0.09	0.768
Latency to leave release point	Angular separation	-0.013	0.006	5.20	0.023
	Angular separation^2	0.000	0.000	6.53	0.011
	Latency to respond	0.000	2.320E-04	0.00	0.948
	Intercept	214.755	114.408	3.52	0.061
Latency to respond	Block	4.670	3.388	1.90	0.168
	Age	-17.179	10.063	2.91	0.088
	Angular separation	0.065	0.124	0.27	0.600
	Intercept	51.545	127.984	0.16	0.680
	Block	6.791	4.122	2.71	0.100
	Age	0.496	10.760	0.00	0.960
	Angular Separation	0.062	0.149	0.17	0.680

Pearson product-moment correlation $r = 0.804$, $t = 23$, $df = 302$, $P < 0.001$). In two-choice tests, subjects responded in 86.8% (66 of 76) of trials, while that percentage declined to 61.8% (47 of 76) in four-choice tests, 48.1% (37 of 77) in six-choice tests, and 44.0% (33 of 75) in eight-choice tests. The quadratic effect of the number of stimuli on the probability of response was marginally nonsignificant ($\beta = 0.013$, $W = 5.74$, $P = 0.017$; Figure 4b).

When subjects did respond to playback, they became significantly less likely to choose the preferred stimulus as the number of stimuli increased ($\beta = -0.098$, $W = 45.18$, $P < 0.001$; Figure 4c). In two-choice tests, subjects performed similarly to those in the preliminary experiment that established the preference for 7-pulses over 2-pulses (binomial test, $H_A: \theta \neq 0.500$; $P = 0.009$; 95% CI = [0.540, 0.778]). In the four-choice tests, subjects continued to choose the speaker broadcasting the preferred stimulus significantly more often than expected by chance (binomial test, $H_A: \theta \neq 0.250$; $P = 0.01$; 95% CI = [0.283, 0.578]). However, female signal discrimination was not better than chance in six- and eight-choice tests (Figure 4b). Subjects chose the preferred signal in only 6 of 37 six-choice tests (binomial test, $H_A: \theta \neq 0.167$; $P = 1.0$; 95% CI = [0.062, 0.320]) and 4 of 33 eight-choice tests (binomial test, $H_A: \theta \neq 0.125$; $P = 1.0$; 95% CI = [0.034, 0.282]). Adjusting the probability of choosing each stimulus for the number of representations of that stimulus in each trial reveals the changing slope of female preference functions as the number of stimuli increases (Figure 5).

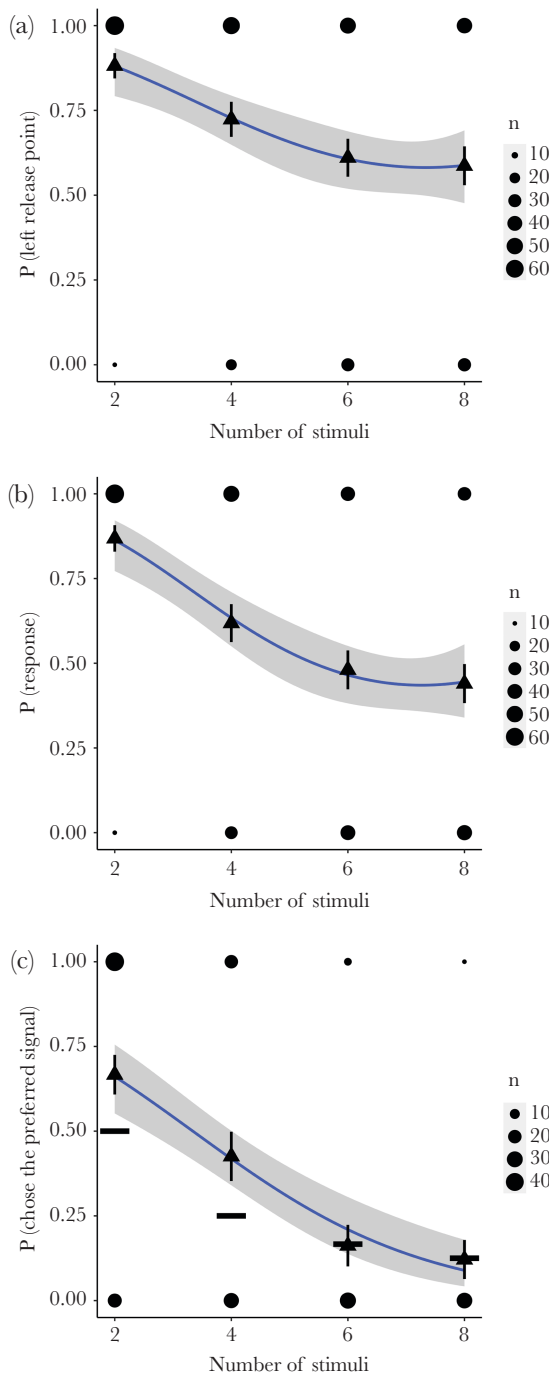
The number of stimuli had no effect on either the latency to leave the release point ($\beta = -1.43$, $W = 0.09$, $P = 0.762$; mean = 133 s, median 59 s, range: 1–596 s) or the latency to respond to stimuli ($\beta = -2.56$, $W = 0.18$, $P = 0.669$; mean = 174 s, median = 52 s, range = 4–659 s). There was no significant effect of response latency on the probability of choosing the 7-pulse stimulus ($\beta = 0.000$, $W = 2.56$, $P = 0.110$), indicating that listening for longer before making a decision did not improve signal discrimination. Despite the expectation that crickets might improve

signal-to-noise ratios by moving throughout the arena, individuals tended not to move continuously without indicating a choice; across the experiment, only 5 trials (1.6%) of 5 unique crickets ended with the receiver moving within the arena but without indicating a playback speaker by the end of 11 min.

Angular separation experiment

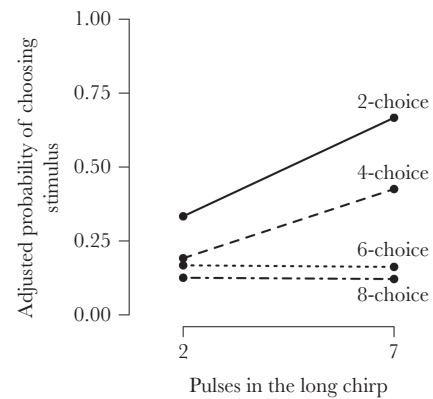
We conducted a series of two-choice tests with speakers at decreasing angular separations chosen to mirror the spatial relationship between any two adjacent speakers in the multi-choice experiment. Across the angular separation experiment, subjects responded to playback in 173 of 212 (81.6%) of two-choice tests. Of the 39 trials in which subjects did not respond to playback, 26 tests of 15 unique receivers ended without the subject leaving the release point. The number of tests that ended with a receiver having left the release point without indicating a choice were 5, 3, 2, and 3 in the 180, 90, 60, and 45° tests, respectively.

After Bonferroni correction, there were no significant effects of the angular separation between playback speakers on any measures of receiver response, including the probability of leaving the release point, responding to playback, or choosing the preferred, 7-pulse stimulus (Table 2). Marginally nonsignificant linear ($\beta = -0.13$, $W = 5.20$, $P = 0.023$) and quadratic ($\beta = 6.88e-5$, $W = 6.53$, $P = 0.011$) effects of the angular separation of speakers on the probability of choosing the preferred stimulus suggested a trend toward better signal discrimination at the smallest and largest angles of separation (Figure 6c). That trend was supported by the binomial tests. At the largest (180°) and smallest (45°) angular separations, receivers discriminated between stimuli with different numbers of long chirp pulses above chance levels (binomial tests: 180° $H_A: \theta \neq 0.500$; $P < 0.001$; 95% CI = [0.659, 0.914]; 45° $H_A: \theta \neq 0.500$; $P = 0.004$; 95% CI = [0.572, 0.850]). Receivers also chose the preferred signal more often than expected by chance at 60° of separation (binomial test: $H_A: \theta \neq 0.500$; $P = 0.05$; 95% CI = [0.501, 0.795]). However, at an angular separation of 90°,

**Figure 4**

Data from the multi-choice experiment. The probability of leaving the release point (a), the probability of response (b), and the probability of choosing the preferred, 7-pulse stimulus (c) declined with increasing numbers of stimuli. Raw (binary) data points (filled black circles) are scaled by the number of responses. Triangular symbols and error bars show means and standard errors. Blue lines and grey shading show the lines of best fit based on generalized linear models. In panel (c), the horizontal black bars show the null expectation, that is, the probability of responding to the preferred signal by chance for each number of stimuli.

which corresponded to the angular separation of adjacent speakers in our 4-choice experiment, receivers performed no better than chance at the signal discrimination task (binomial test: $H_A: \theta \neq$

**Figure 5**

Female preference functions for the number of long chirp pulses based on the adjusted probability of choosing each stimulus. The adjusted probability of choosing a stimulus is calculated by dividing the raw probability of choosing the stimulus by the number of representations of that stimulus in a given trial, such that in all trials, the probability of choosing the 7-pulse signal is divided by 1. The raw probability of choosing the 2-pulse stimulus was divided by 1, 3, 5, and 7 in the two- (solid line), four- (dashed line), six- (dotted line), and eight-choice (dash-dotted line) tests, respectively. Note that the adjusted probabilities sum to 1 only in the two-choice tests. Subjects preferred the 7-pulse stimulus above chance levels in the two- and four-choice tests, but showed no preference in the six- and eight-choice tests.

0.500; $P = 1.0$; 95% CI = [0.355, 0.667]). The angular separation between speakers did not explain the results from the multi-choice experiment (compare triangular symbols to horizontal black bars in Figure 6c).

DISCUSSION

In a series of signal discrimination tasks with two, four, six, or eight alternatives, we observed that receivers became less likely to respond phonotactically to any song stimulus as the number of simulated signalers increased. Moreover, the well-documented mating preference for more long chirp pulses eroded as the number of alternative stimuli increased and was not rescued by longer listening times. We confirmed that these changes in receiver behavior were not explained by the change in angular separation between playback speakers. In nature, individual receivers frequently make mating decisions in environments much more socially and physically complex than our assay, where the sounds produced by conspecific and heterospecific signalers, combined with noise from other biotic and abiotic sources, can impede signal reception (Wiley 2015). Yet studies of female mating preferences for acoustic signals typically use single- or two-stimulus paradigms under highly controlled conditions that fail to replicate the complexity of natural environments. Our results suggest that individual receivers are likely to express their mating preferences less often in natural environments with realistic levels of social complexity than they do under simplified laboratory conditions. Two-alternative forced choice tests performed in otherwise quiet conditions are likely to overestimate the strength of sexual selection that occurs in nature. Noise might provide a partial explanation for the maintenance of variation in male phenotypes in the face of apparently strong, directional sexual selection (Kirkpatrick and Ryan 1991; Pomiankowski and Møller 1995).

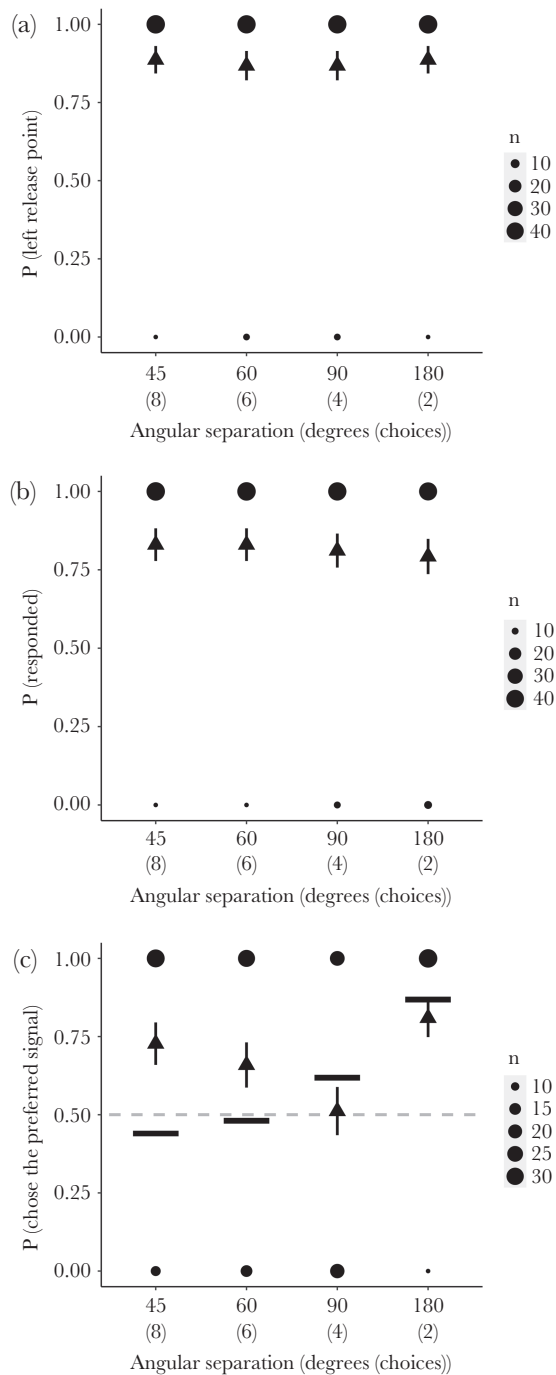


Figure 6

Data from the angular separation experiment. The probability of leaving the release point (a), the probability of response (b), and the probability of choosing the preferred, 7-pulse stimulus (c) as a function of the angular separation between speakers (with corresponding number of choices from the multi-choice experiment in parentheses below the x-axis). Raw (binary) data points (filled black circles) are scaled by the number of responses. Triangular points and error bars show means and standard errors. In panel (c), the horizontal black bars show the measured probability of choosing the 7-pulse stimulus in the multi-choice experiment with an equivalent angular separation of speakers.

The decrease in responsiveness and signal discrimination that we observed in the multi-choice experiment must be interpreted in light of the neural mechanisms of signal recognition and

discrimination, which are well understood in field crickets and depend on remarkably few neurons (Wohlers and Huber 1978; Pollack 1986; Schildberger and Hörner 1988; Stabel et al. 1989; Horseman and Huber 1994). Cricket auditory systems are tuned to the temporally-patterned signals of conspecific males, with directional hearing accomplished by comparing the sound pressures of signals arriving at each of the animal's ears (Hill and Boyan 1976). When a receiver hears two signals from opposite sides of her body, auditory neurons faithfully represent the temporal pattern of the two signals as long as the two sound sources are adequately spaced apart (Pollack 1986). However, as the angular separation of the sound sources from the animal's midline decreases, neuronal representations of the two stimuli become less readily distinguishable and are noticeably disrupted at around 15° from the animal's midline (30° separation between speakers); moreover, the effect of the sound source's azimuth grows stronger as the amplitude of playback increases (Pollack 1986). We played signals back at relatively high, but realistic amplitudes (80 dB SPL) and surrounded receivers with signals produced at equal amplitudes and equal starting distances from the receiver. Thus, it could make sense that the spatial arrangement of speakers in the multi-choice experiment might present challenges for crickets during phonotaxis; in that case, data from the angular separation experiment should mirror the results in the multi-choice experiment: decreasing responsiveness and signal discrimination with decreasing angles of separation. Data did not support that prediction. After correction for multiple testing, GEE uncovered no significant predictors of any metric of female response; this might be because the sample size in the angular separation experiment was somewhat smaller than in the multi-choice experiment (53 versus 77 crickets, respectively). However, binomial tests showed that crickets performed well above chance levels at discriminating differences in stimuli separated by as little as 45°. The only angular separation at which they did not distinguish above chance levels was 90°. The spatial acuity of hearing in crickets is not directionally uniform; rather, cricket hearing is most spatially acute hearing when sounds are directly in front of or directly behind them, and least acute in the region toward their sides (Wytenbach and Hoy 1997). That may explain why receivers chose seemingly at random when two stimuli were presented at right angles to each other in the angular separation experiment. Interestingly, receivers did choose the preferred stimulus more often than expected by chance in four-choice tests, in which all speakers were separated by 90°. We hypothesize that this is because, as a receiver oriented toward any given speaker from the approximate center of the arena, that movement was likely to bring two speakers into the areas in front of and behind the cricket, where hearing was more acute. In any case, the angular separation of speakers did not explain the results of the multi-choice experiment.

While acoustic masking interference is one possible cause for the changes in female responses observed in the multi-choice experiment, the data are also consistent with the hypothesis that subjects are experiencing choice overload. Choice overload is a phenomenon in animals, including humans, whereby the cognitive load or confusion caused by an overwhelming number of options prevents individuals from choosing any option or decreases choice quality (Iyengar and Lepper 2000; Hutchinson 2005; Lenton and Francesconi 2011; Chernev et al. 2015). In some acoustically communicating animals, receivers become less responsive and less selective as the number of signaling males (i.e., available options) increases, even with very small group sizes (Gerhardt 1987; Telford et al. 1989; Bishop et al. 1995; Hutchinson 2005; this study). Imperfect choice (receiver error) due to confusion may allow

low-quality signalers to gain matings and might partially explain why mating skew is less pronounced in larger leks (Johnstone and Earn 1999). Choice overload represents an important, nonacoustic example of a source of noise in the broadest sense of the term: anything that inhibits signal detection or discrimination (Shannon 1948; Wiley 2015).

The perception of risk may also factor into why receivers are more likely to reject all signalers in tests with more available options (Dougherty and Shuker 2015). Individuals that perceive they are unlikely to have another opportunity to mate later may be more likely to accept an unattractive or otherwise inappropriate mate (Berglund 1994; Jennions and Petrie 1997). Our observation that receivers were less likely to respond phonotactically when there were higher numbers of stimuli in the local environment could be explained by receivers' perception that available prospective mates are plentiful (Shelly and Bailey 1992). Australian field crickets are known to use cues from the acoustic environment to mediate many aspects of their reproductive biology and sexual behavior, including selectivity and responsiveness to song (Bailey and Zuk 2008; Swanger and Zuk 2015; Lierheimer and Tinghitella 2017; Gurule-Small and Tinghitella 2018), but much of the research examining how acoustic cues mediate plasticity in receiver behavior examines the long-term effects of exposure to song during juvenile or early adult development. It is less clear how receivers might perceive the risk of remaining unmated in a shorter-term scenario like our mate choice assay, in which individuals sequentially experienced the two-, four-, six-, and eight-choice assays in random order within a few hours.

Outside the laboratory, animals often communicate in mixed-species choruses where they must solve “cocktail-party-like” problems—that is, perceive relevant signals in noisy social situations (Gerhardt and Huber 2002; Bee and Micheyl 2008; Schmidt and Römer 2011). One solution to the cocktail party problem is spatial release from masking, a phenomenon characterized by improved receiver performance when the sources of a signal and the background noise are separated in space (Schmidt and Römer 2011; Nityananda and Bee 2012; Schmidt and Balakrishnan 2015). However, some insects may experience little or no spatial release from masking, depending on characteristics of their auditory systems, which function differently and evolved independently from the auditory systems of vertebrates in which spatial release from masking has been primarily studied (Cherry 1953; Bronkhorst 2000; Bee 2007; Bee and Micheyl 2008; Nityananda and Bee 2012; Albert and Kozlov 2016; Brunnhofer et al. 2016; Göpfert and Hennig 2016; Lee and Mason 2017; Manley 2017). Whether spatially separated sound sources in natural insect choruses produce enough noise to alter receiver behavior is thus an interesting but understudied question. Many laboratory studies may not appropriately reconstruct masking effects of noise because they fail to take into account that noise-generating sound sources in the real world are distributed in space (Schmidt and Römer 2011). An advantage of the present study is that we have effectively generated the effects of masking noise as an emergent feature of spatially separate sound sources.

Because chorus noise is an emergent property of spatially separated sound sources that are subject to attenuation as a result of geometric spreading (Simmons 1988; Römer 1992; Kostarakos and Römer 2010), the intensity of chorus noise is expected to vary as a function of, among other factors, chorus density. In natural choruses, *T. oceanicus* males have a minimum nearest-neighbor distance of 0.9 m and a mean nearest-neighbor distance of between 3.2 and

3.8 meters (Cade 1981), thus we have simulated a somewhat denser chorus than is expected to occur in the field. In the present study, we maintained a constant initial distance between the receiver and each simulated signaler (1.0 m). The linear distance between any given speaker and its nearest neighbor varied between tests with different numbers of stimuli (angular separations), decreasing from 2.0 m in the 2-choice (180°) test to 1.4 m, 1.0 m, and 0.77 m in 4- (90°), 6- (60°), and 8-choice (45°) tests, respectively. It is interesting to note that the minimum documented nearest-neighbor distance in nature (0.9 m) falls at approximately the nearest-neighbor distances in our 6-choice tests, and that this is also the point at which receiver signal discrimination broke down. Receivers expressed their preference for higher numbers of long chirp pulses in 4-choice tests but fared no better than chance at the signal discrimination task in 6-choice tests. It is plausible that past selection has favored individual signalers that maintain an adequate distance from their nearest neighbors to allow signal recognition by receivers.

A limitation of the present study, and of phonotaxis experiments in general, is that it is impossible to ascertain the extent to which receivers are sampling and comparing signals at a distance because our metric of signal discrimination was dependent on the receiver approaching a signal. Receivers may listen to multiple signals without moving, and therefore without affecting response metrics. Sampling male signals by moving through space may be advantageous because it is expected to increase the signal-to-noise ratio of a focal signal relative to the background chorus noise. In our experiment, subjects tended not to move continuously throughout the arena without making a decision; very few trials ended with a cricket moving throughout the arena without responding to any single playback speaker. We noted no increase in response latency or latency to leave the release point in noisier environments, and there was no evidence that listening for longer improved signal discrimination. Receivers simply became both less likely to approach speakers broadcasting calling song and less likely to approach preferred signals. In *T. oceanicus* and other gryllid crickets, calling song is used for long-distance mate attraction. Upon being approached by a female, males typically initiate courtship, which involves a distinct acoustic signal as well as chemosensory signals (cuticular hydrocarbons; Balakrishnan and Pollack 1996; Rebar et al. 2009; Thomas and Simmons 2009; Simmons et al. 2013). The present study suggests receivers may not approach calling song or exercise mate choice on the basis of calling song as often as previously supposed. Nevertheless, sexual selection may still act on other, shorter-range sexual signals, should individuals find themselves in close proximity to one another without the mediation of calling song (e.g., through random walking; Balenger and Zuk 2015). We note that sexual selection may also act indirectly on calling song phenotypes through correlations among phenotypes within individuals.

Receivers have preferences for a broad array of signals that carry biologically relevant information, and more than a century of research has sought to uncover how receiver behavior imposes the selection that shapes signals and signalers. However, the fact that receivers have mating preferences for acoustic signals does not guarantee the expression of those preferences in natural communication contexts. Here, we show that a relatively small number of conspecific signals can produce the emergent effects of chorus noise, impairing receiver signal recognition and discrimination in an acoustically communicating animal. Thus, to the extent that acoustic communication mediates mating, we conclude that receivers are likely to exert weaker selection on signalers in noisy environments. While this study advances our understanding of

receiver behavior, we note that it also falls short of the kind of complexity receivers face in nature because the stimuli represented two extremes of a single signal trait, and thus, receivers were faced with a relatively straightforward discrimination task. In nature, receivers must discriminate among signals that vary in multiple dimensions (Bentsen et al. 2006; Tanner et al. 2017) while also contending with other sources of noise, which need not necessarily be acoustic, including the natural within-individual variation in signal production that can mask between-individual variation in signals (Tanner and Bee 2019; Tanner and Bee 2020b). Noise is an important, intrinsic part of communication systems and further study is needed to understand its impact on receivers and the selection mediated by their behavior.

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AUTHOR CONTRIBUTIONS

Both authors conceived of and designed the study, contributed to the interpretation of results, critically revised the manuscript, and approved the final version. J.C.T. collected, curated, and analyzed the data, and wrote the original draft of the manuscript.

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