

Predicting acoustic orientation in complex real-world environments

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SUMMARY

Animals have to accomplish several tasks in their lifetime, such as finding food and mates and avoiding predators. Animals that locate these using sound need to detect, recognize and localize appropriate acoustic objects in their environment, typically in noisy, non-ideal conditions. Quantitative models attempting to explain or predict animal behaviour should be able to accurately simulate behaviour in such complex, real-world conditions. Female crickets locate potential mates in choruses of simultaneously calling males. In the present study, we have tested field cricket acoustic orientation behaviour in complex acoustic conditions in the field and also successfully predicted female orientation and paths under these conditions using a simulation model based on auditory physiology. Such simulation models can provide powerful tools to predict and dissect patterns of behaviour in complex, natural environments.

Key words: phonotaxis, acoustic orientation, real-world environments, biomimetic simulation model.

INTRODUCTION

Animals have to accomplish several tasks in their lifetime, such as finding food and mates and avoiding predators, typically in noisy, non-ideal conditions. The sensory and neural mechanisms underlying many of these behaviours have been extensively studied in a number of taxa (Camhi, 1984). Several of these are now understood to the extent that quantitative modelling approaches have been successfully used to mimic behaviour (Webb, 2000). These models attempt to mimic the sensory and neural systems that control behaviour and ask whether they are sufficient to explain it (Webb, 2001). The models are, however, typically tested under conditions that are simpler than those faced by animals in their natural environment. Neuroethological modelling studies, which take a bottom-up approach to explaining behaviour, are based on the premise that a complete understanding of the underlying mechanisms should allow us to predict behaviour in any situation, including complex real-world conditions (Dean, 1998). The testing of models is, therefore, inadequate without quantitative comparisons between the predictions of the models and the behaviour of animals in real-world conditions.

Field cricket phonotaxis has been investigated in several laboratory studies, which have shown that, when faced with multiple song sources of their own species, female crickets preferentially approach louder songs (Roemer, 1998; Hedwig and Poulet, 2005). Laboratory experiments are, however, carried out under ideal conditions and the selectivity observed under these conditions cannot easily be extrapolated to the field, where songs are attenuated and their temporal patterns degraded by the environmental transmission channel (Roemer, 1998). In addition, several males often call simultaneously, interfering with each other's song (Feng and Schul, 2006). This creates a complex acoustic environment in which sound localization becomes a challenging task, and little is known about orientation abilities under these conditions. Field experiments using pitfall traps show that female crickets prefer louder songs (Roemer, 1998; Gerhardt and Huber, 2002). However, since these experiments only recorded capture data, one cannot infer much about orientation abilities from them.

Many aspects of the mechanisms underlying cricket phonotaxis are understood across multiple levels: biophysical (Michelsen, 1998), neurobiological and behavioural (Pollack, 1998; Hedwig, 2006). This has allowed for the creation of robotic models (Webb, 1995; Reeve et al., 2005); however, these models have not been validated in realistic, multi-source field conditions (Webb, 2006).

We previously developed a simulation model of field cricket walking phonotaxis based on auditory physiology and phonotactic walking behaviour observed in the laboratory (Mhatre and Balakrishnan, 2007). This simulation model attempts to capture the perception of calling song by field crickets using information on the tuning of the cricket ear, its directional properties and the ability to selectively attend to louder songs; it also models the threshold and saturation of the auditory receptors (Pollack, 1986; Pollack, 1988; Michelsen, 1998; Pollack, 1998). Virtual females in this model respond to perceived sounds by moving towards the louder sound. Their motor behaviour is stochastic and is modelled on the basis of data collected in our previous laboratory experiments under closed-loop conditions in which females were exposed to two calling songs at different absolute and relative sound pressure levels (SPLs) (Mhatre and Balakrishnan, 2007). This model was able to successfully simulate the phonotactic orientation behaviour of real females at the population level in the laboratory experiment as well as in a two-source field experiment (Mhatre and Balakrishnan, 2007). In the present study, we show that this simulation model can successfully predict acoustic orientation behaviour in multi-source field conditions.

MATERIALS AND METHODS

Set up and stimuli

Experiments were carried out in the natural habitat of *Plebeigryllus guttiventris* (Walker), which consists of hard ground sparsely covered with herbs and forbs. In the area being videotaped, vegetation cover was almost completely removed in order to allow us to view the females clearly. We believe that the environment created by this manipulation is not unnatural since several of the natural habitats where we have observed these crickets consist of

bare ground completely devoid of vegetation. The effects on the song due to sound reflections from the ground, such as echoes, and the decrease in song amplitude due to the ground effect were not minimised in any way. Other effects such as amplitude fluctuations due to atmospheric turbulence were also present. Sound attenuation levels measured in the experimental areas were similar to those measured previously (Mhatre and Balakrishnan, 2006) in the same habitat with intact vegetation.

Experiments were carried out between December and February (the breeding season) 2005 and 2006 (the breeding season) at peak activity time (18.30–20.00 h). Ambient temperatures ranged from 18°C to 22°C. Stimuli were synthesized using a single chirp from a *P. guttiventris* song recorded at 21°C (Mhatre and Balakrishnan, 2007). The temporal pattern used was appropriate for this temperature (carrier frequency=4.9 kHz, chirp duration=180 ms, chirp period=339±32 ms) (Mhatre and Balakrishnan, 2006). Stimuli were broadcast from either a pair of Creative speakers (Creative Labs Inc., Singapore) (frequency range: 100 Hz–15 kHz) or these in combination with Philips BA109 loudspeakers (Amsterdam, The Netherlands) (frequency range: 100 Hz–18 kHz). These two pairs of speakers received input from two independent CD players (AIWA Co. Ltd, Tokyo, Japan), which both played out two *P. guttiventris* songs, which were aphasical with respect to each other, as is the case with simultaneously singing males (Mhatre and Balakrishnan, 2006). The songs were looped and started at random points within the loop for each trial. The speakers were covered with black cloth and placed on their sides, partially buried in the ground to reduce visibility and mimic the calling behaviour of real male crickets that call from ground level.

The broadcast SPLs of the speakers at source (10 cm from the speaker) and at the positions of the females are indicated for each experiment in the figures, as are the initial release positions and orientations. The positions of the speakers were selected based on a map of a real chorus of males observed in the field, and the distances between males reflect observed intermale distances (Mhatre and Balakrishnan, 2006). The particular chorus was selected as it provided a situation in which a female might hear four simultaneously calling males. The SPLs of the speakers were based on measurements of the calling song SPLs of real males. Males produce calling song at an average of 75±4.6 dB SPL (Mhatre and Balakrishnan, 2006). We chose broadcast SPLs from the centre, as well as approximately one and two standard deviations of this distribution of song SPLs. The SPLs from the speakers, as measured at the release positions, were all above behavioural threshold and females could potentially hear all speakers simultaneously and should experience song pattern masking similar to field conditions (Mhatre and Balakrishnan, 2006). The broadcast SPLs (root mean square, RMS at the fast setting) of the four speakers were measured one at a time using a Brüel & Kjær microphone (type 4189) and Integrating Sound Level Meter (Observer 2260) with a one-third octave band-pass filter (Brüel & Kjær Sound and Vibration Measurements A/S, Naerum, Denmark) centered at 5 kHz at ground level, with the microphone facing the active speaker at a distance of 10 cm and at the female release position in each experiment. Each experiment was carried out in two physically separate outdoor locations with the setup rotated by 180 deg. to control for directional bias due to non-acoustic cues.

Animals

Virgin females from a laboratory culture were used during experiments. The cultures were maintained, and females chosen and prepared for the experiment as described previously (Mhatre and

Balakrishnan, 2007). Females were tested further only if they responded to the softest broadcasting single speaker. The single speaker control was presented from the left for approximately half of the females and from the right for the remaining half. Females were given a rest of at least 10 min between trials. A set of 40 females was tested with both two and four speakers active. The order of presentation was varied, and half the females were presented with four speakers active before two speakers active and *vice versa* for the remaining half.

An independent set of 38 females was used to test for the effects of initial orientation. Nineteen females were released with their initial position rotated by 180 deg. and 19 females with their initial position rotated by 30 deg. to the left. Thirty-nine females were used to test for the effect of different release positions and orientations, 20 females from release position 1 (RP1) and 19 females from release position 2 (RP2). Some of the females tested in the orientation experiment were re-tested in the release position experiment. Females were only tested once a day.

Data analysis

Female paths were recorded and digitized (Mhatre and Balakrishnan, 2007), and a note was made of which speaker each female reached. The paths were digitized until the background subtraction algorithm could not discern the female. In some cases, the digitized path ended before the female reached the speaker; however, this could be observed in the video and was noted separately. The endings of such paths are indicated by dotted lines in the figures. The number of females reaching the speakers was compared between experiments using a chi-squared test using Statistica (1999; Statsoft, Inc., Tulsa, OK, USA).

A logistic multiple regression was carried out in R (version 2.5.1; R Foundation for Statistical Computing, Vienna, Austria) with the following independent variables; the SPL of each speaker at source, SPL at the release position of the female, and distance to each speaker from release. Since individual females were tested in more than one experiment, we used data only from the experiments front, RP1 and RP2 in order to prevent pseudoreplication due to repeated testing of individuals. Another reason for the exclusion of data from the other experiments was because they showed results that were not greatly different from the experiment with the frontal orientation. Female arrival or non-arrival at each speaker was the categorical dependent variable. Since each female contributed four data points to the analysis, a linear mixed-effects model was used with female identity as a grouping variable in order to control for pseudoreplication (Crawley, 2002). The analysis was first carried out with interaction effects, which were not statistically significant. The analysis was then carried out without the interaction effects and the results from this analysis are reported.

To compare path forms we calculated the path vectors (Batschelet, 1981). We delineated pauses within the paths of the females and calculated average position within a pause. Pauses were defined as in an earlier study (Mhatre and Balakrishnan, 2007) except that the cutoff was raised to 0.2 cm due to the lower resolution of these videos. The angle of displacement between pauses was determined, and path vectors were calculated for both the real and simulated paths. Path vectors were compared between experiments and between a single experiment and a simulation run using a Mardia two-sample test for bivariate data followed by a Mardia–Watson–Wheeler test (χ^2 test statistic for $N>17$) (Batschelet, 1981). This non-parametric test was used as it does not assume a von Mises distribution of vectors.

Simulations (for details, see Mhatre and Balakrishnan, 2007) mimicking the real experiments, with the same number of paths

in each run were performed in Matlab (V. 6.5, The Mathworks, Inc., Natick, MA, USA). Females who reached within 2 cm of a speaker in the simulation were marked as having reached that speaker. For each experimental scenario we ran 20 simulation runs and measured the mean number of females reaching each speaker and not reaching speakers. These numbers were then compared with the numbers in the experiments with real females using a chi-squared test. Finally, the numbers of real females reaching and not reaching speakers were also subjected to a bootstrap analysis (10,000 iterations) (carried out in Matlab 6.5) to estimate the confidence ranges on the real data, which were then compared with the range of values predicted by the simulation in 20 runs.

RESULTS

We had previously found that females showed a marked preference for the louder of two speakers, which was also loudest at the release position [31 of 40 females reached the louder speaker (Mhatre and Balakrishnan, 2007)]. In the present study, when the number of active speakers was increased to four, females showed reduced orientation towards that speaker, which was still the loudest at the release position (Fig. 1A, two vs four speakers: $\chi^2=6.58$, d.f.=2, $P=0.03$). The number of females reaching the speaker that was loudest at their release position (23/40) was reduced when compared with the two-speaker situation (31/40) and females approached other speakers in significant numbers (Fig. 1A). Therefore, the presence of additional sources can alter the probability of a female reaching

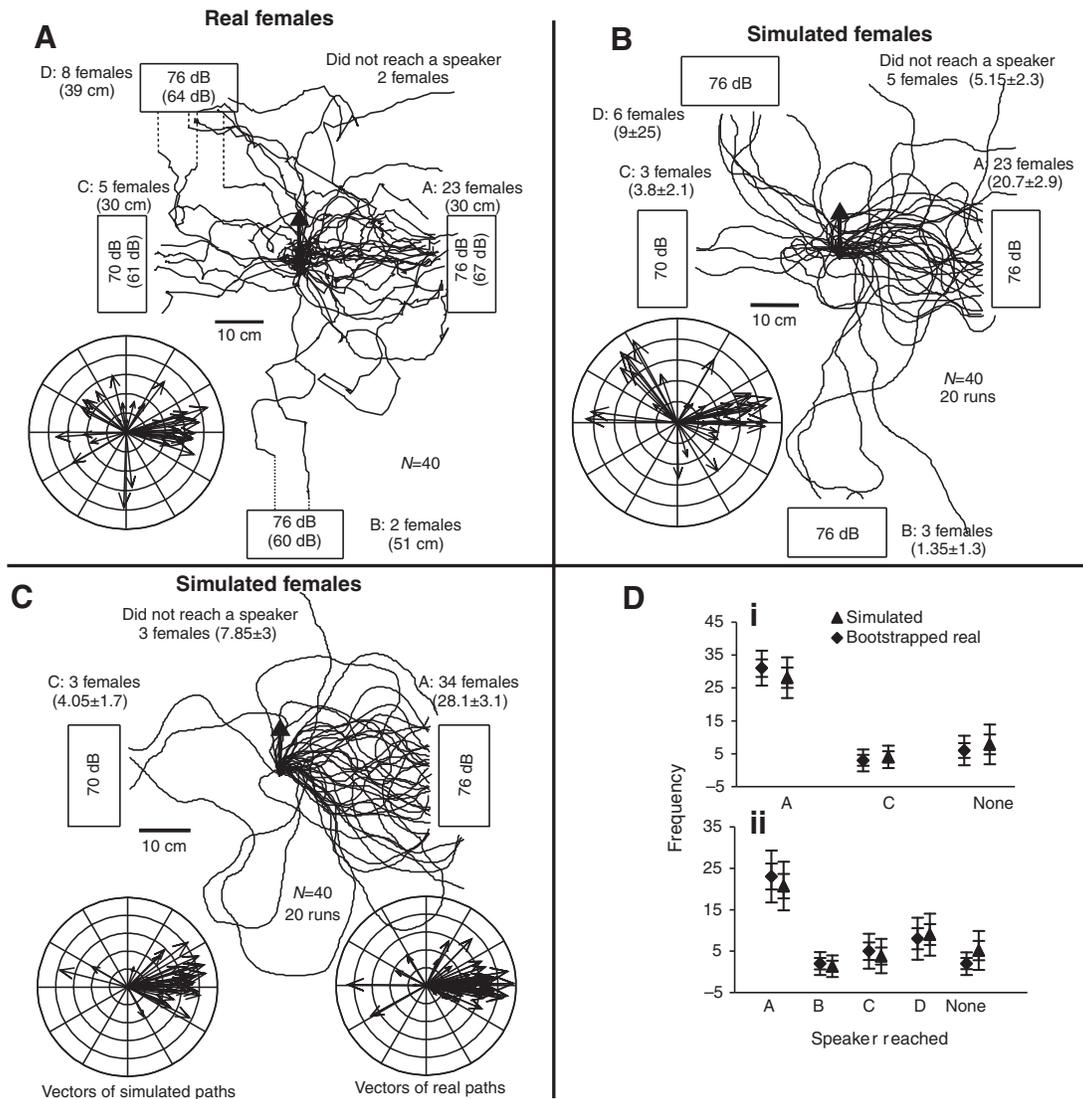


Fig. 1. Cricket phonotaxis in the field with two and four active speakers. (A) Paths of 40 females with a front-facing release orientation, four speakers active. (B) A simulation of 40 phonotactic paths with stimulus conditions identical to A. (C) A simulation of phonotaxis with two active speakers (40 paths, front-facing release orientation). (D) The bootstrapped ranges of frequencies of females reaching each of the speakers with two (i) and four (ii) speakers active and the range predicted by the simulation. The symbols indicate the mean; error bars indicate one and two standard deviations. Path vectors of real and simulated paths are shown as insets in the panels in all figures. Boxes depict speakers with the broadcast SPL indicated within each box. SPLs indicated in parentheses were measured at the release position of the female. The names of the speakers are indicated next to each box depicting the speaker with the distance to the speaker from the release position indicated in parentheses. The mean number (\pm s.d.) of females reaching a speaker in 20 simulation runs of as many paths as in the real data is indicated near to each speaker. The arrow in the central position in A–C indicates the position and the orientation of the female at release.

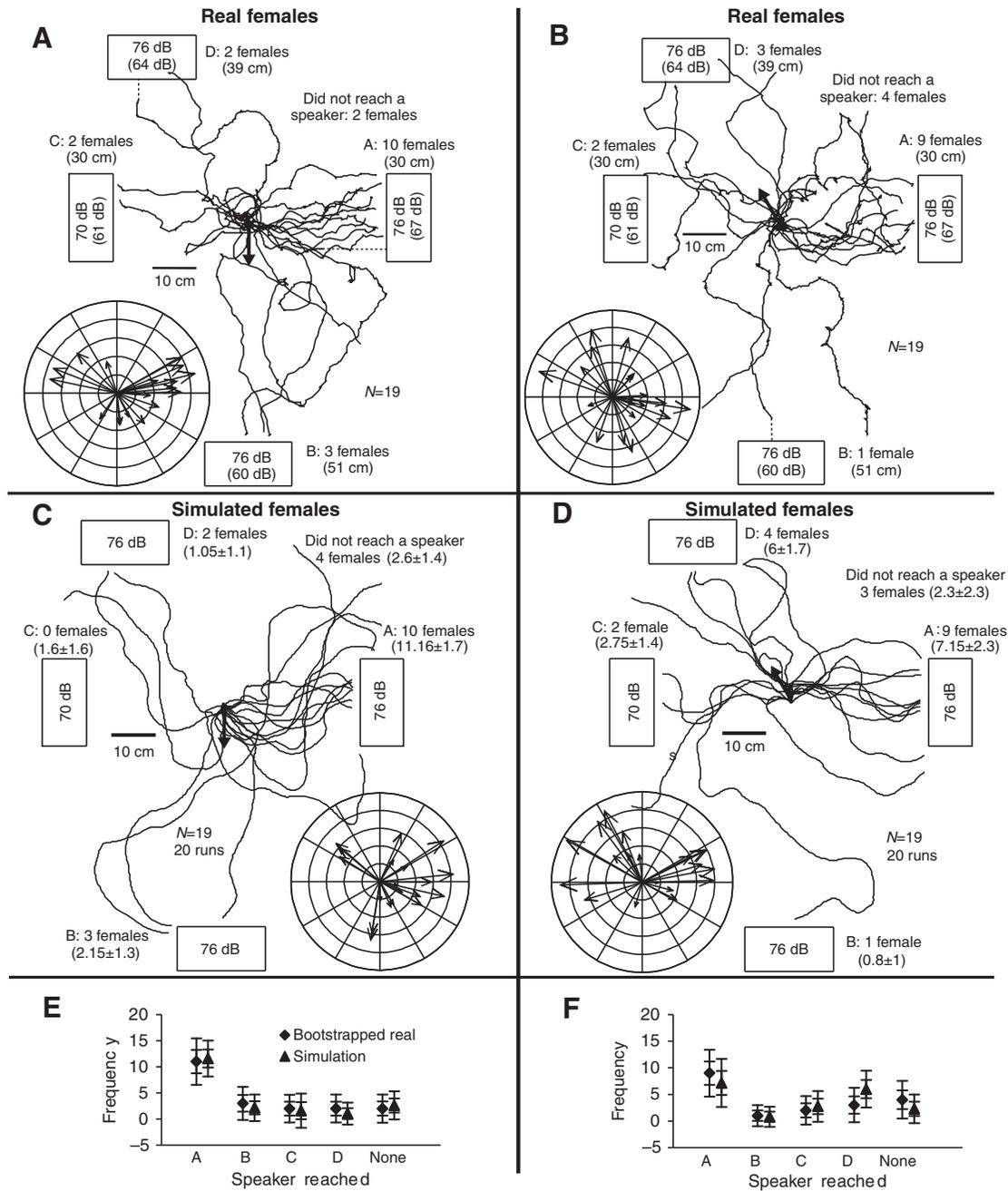


Fig. 2. Effect of initial orientation on phonotaxis. (A) Paths taken by 19 females, backward-facing release orientation, four speakers active. (B) Paths taken by 19 females, leftward-facing release orientation, four speakers active. A simulation of 19 paths: (C) backward-facing release orientation, four active speakers, (D) leftward-facing release orientation, four active speakers. The bootstrapped ranges of frequencies of females reaching each of the speakers and the range predicted by the simulation (E) with the backward-facing and (F) leftward-facing release orientation. All other conventions are as in Fig. 1.

a given sound source, even when it remains the loudest at her initial position. The forms of the paths were also different, as judged by their path vectors, which were more scattered (Fig. 1A,C, insets: $\chi^2=6.34$, $P=0.04$).

The effect of initial orientation was tested using the same configuration of speakers and female release position but with three different release orientations (Fig. 1A and Fig. 2A,B). Orientation behaviour did not alter significantly when females were turned around by 180 deg. at release (Fig. 1A vs Fig. 2A, $\chi^2=6.57$, d.f.=4, $P=0.16$), and path forms were also not significantly different ($\chi^2=0.06$, $P=0.97$). However, when females were tilted by 30 deg.

towards the softer speaker at release, we found a small but significant change in comparison with the front orientation (Fig. 1A vs Fig. 2B, $\chi^2=10.36$, d.f.=4, $P=0.03$) but not the back orientation (Fig. 2A vs Fig. 2B, $\chi^2=5.44$, d.f.=4, $P=0.24$). When females were initially oriented towards the left, we expected that a larger number of females would reach the speaker to the left or in front of them. However, this did not happen; instead, fewer females reached the speaker that was loudest at their release position. Path vectors were not significantly different in either comparison (front vs left, $\chi^2=4.15$, $P=0.12$, back vs left: $\chi^2=1.35$, $P=0.51$), suggesting only a weak overall effect of initial orientation.

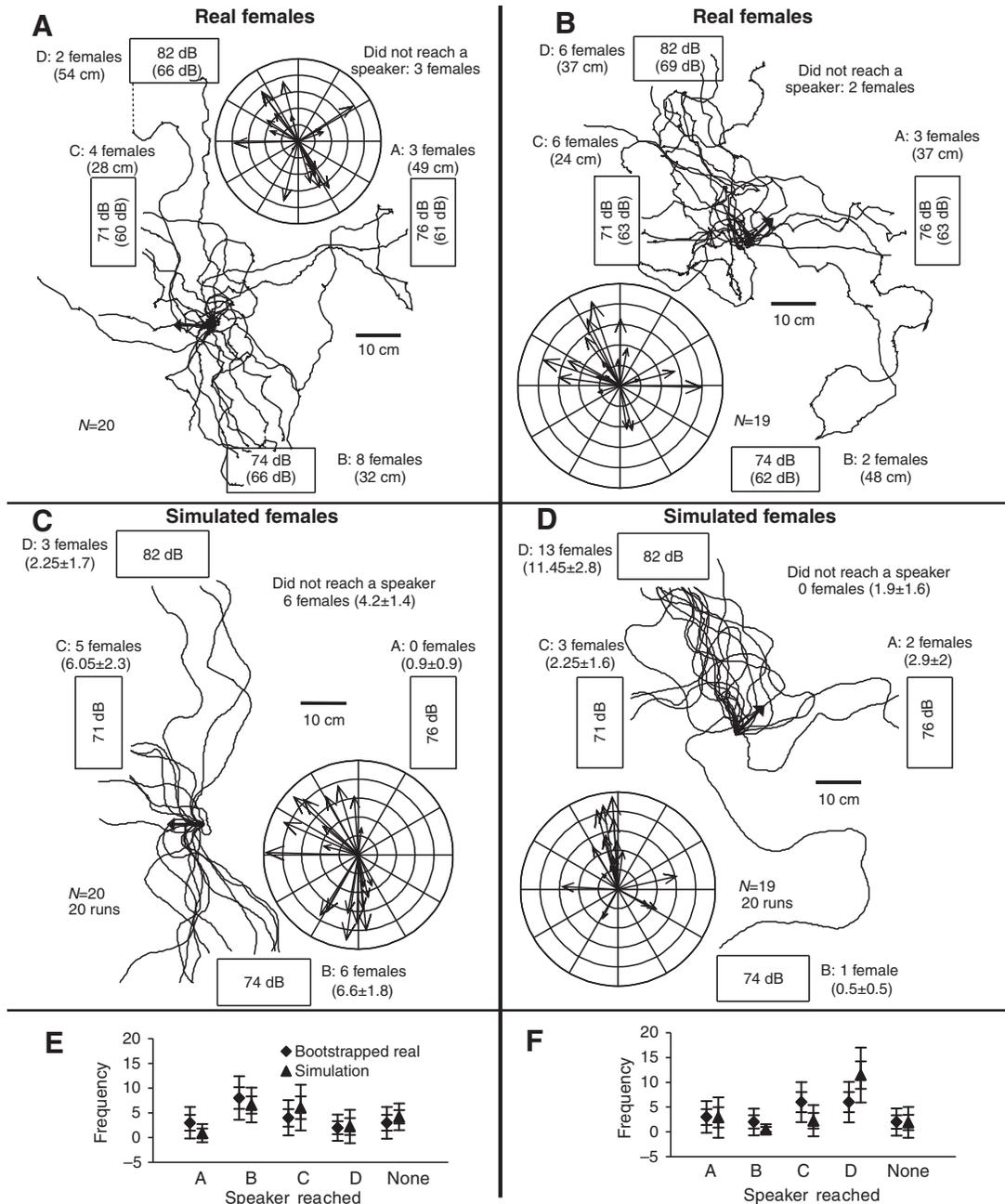


Fig. 3. Effect of initial position on phonotaxis. (A) Paths taken by 20 females with a non-central release position (RP1), four speakers active. (B) Paths taken by 19 females, non-central release position (RP2), four speakers active. (C) A simulation of 20 paths with a non-central release position (RP1), four speakers active. (D) A simulation of 19 paths with non-central release position (RP2), four speakers active. The bootstrapped ranges of frequencies of females reaching each of the speakers and the range predicted by the simulation (E) from RP1 and (F) RP2. All other conventions are as in Fig. 1.

We then changed the broadcast levels of the speakers and used two off-centre release positions (Fig. 3A,B). Females were presented with four active speakers at different distances from the release position, with different broadcast SPLs at source and release positions, allowing us to examine the effects of each of these on female orientation. In the first experiment (RP1; Fig. 3A), the female was released such that two of the speakers (B and C) were nearly equidistant from her position and two speakers (B and D) were heard at equal SPL. In the second experiment (RP2; Fig. 3B), one of the speakers (C) was closest to the female, another speaker (D) was loudest at her position and the other two

speakers were as loud as the closest speaker at the release position. In both experiments there was a speaker that was loudest at source (6 dB louder than the next loudest speaker). As expected from the different release positions, females did not orient towards speakers in similar proportions in the two experiments. When released from RP1, females preferentially oriented towards speaker B, whereas when released from RP2, they oriented towards D and C in equal numbers. Female orientation was significantly different between the two release positions (RP1 vs RP2; $\chi^2=14.50$, d.f.=4, $P<0.01$). Path vectors, were however, not significantly different, possibly due to the large spread of angles

(RP1 vs RP2; $\chi^2=1.67$, $P=0.43$). In RP1, neither the two speakers that were loudest at the release position nor the two that were equidistant received equal numbers of females (Fig. 3A). In RP2, the speaker that was loudest at release received as many females as the closest speaker (Fig. 3B). The speaker that was loudest at source did not receive the most females in either experiment.

In order to decipher the influences of speaker SPL at source, at release position of the female and speaker distance, data from three experiments [front (Fig. 1A), RP1 and RP2 (Fig. 3A,B)] were combined and subjected to a logistic multiple regression analysis. The only significant predictor of the probability of reaching a speaker was the SPL of that speaker at the release position (SPL at release, $t=2.24$; $P=0.02$). The broadcast SPL and the distance of speakers from the release position were not significant predictors of the probability of a female reaching a speaker (SPL at source, $t=-0.72$; $P=0.47$; distance, $t=-0.45$, $P=0.65$). The first experiment had twice as many females as the experiments with RP1 and RP2, potentially biasing the outcome of the regression analysis. To test for this we removed 20 randomly selected females from the first experiment and re-ran the analysis on this truncated data set. This was repeated five times. In two out of the five analyses, SPL of a speaker at release was not a significant predictor of the probability of a female reaching a particular speaker ($t_1=1.56$, $P_1=0.12$; $t_2=2.14$, $P_2=0.03$; $t_3=1.58$, $P_3=0.12$; $t_4=2.43$, $P_4=0.02$; $t_5=2.39$, $P_5=0.02$).

Another approach to understanding and predicting phonotaxis behaviour that can be generalized to any number and configuration of active sound sources is a dynamic simulation model based on the known physiology of the cricket auditory system. We tested the predictions of a simulation model that we recently proposed against behaviour observed in the experiments from the present study (Mhatre and Balakrishnan, 2007). As shown before (Mhatre and Balakrishnan, 2007), the model was able to correctly predict female preference in response to two active speakers (simulated vs real outcomes; Fig. 1C; $\chi^2=1.01$, d.f.=2, $P=0.60$). To estimate the confidence intervals on the frequency of females reaching each speaker, we bootstrapped the data 10,000 times and compared the range predicted by the simulation with the bootstrapped range. The resulting frequency ranges overlapped considerably (Fig. 1D, i). The results of the simulation and those using real females were also similar in terms of path forms; path vectors produced by a run of the simulation were similar to those of real females (Fig. 1C; $\chi^2=0.21$, $P=0.90$).

The simulation was then used to predict female behaviour using four active speakers. It was able to predict female preference from the central release position in all release orientations (Fig. 1B vs Fig. 1A, front, $\chi^2=2.98$, d.f.=4, $P=0.56$; Fig. 2C vs Fig. 2A, back, $\chi^2=1.65$, d.f.=4, $P=0.80$; Fig. 2D vs Fig. 2B, left, $\chi^2=3.49$, d.f.=4, $P=0.48$). The frequency ranges predicted by the simulation and the bootstrapped real data showed considerable overlap (Fig. 1D and Fig. 2E,F). The path vectors produced by a run of the simulation model were also similar to the real path vectors (Fig. 1B inset vs Fig. 1A inset, front, $\chi^2=0.09$, $P=0.96$; Fig. 2C inset vs Fig. 2A inset, back, $\chi^2=0.32$, $P=0.85$; Fig. 2D inset vs Fig. 2B inset, left, $\chi^2=3.35$, $P=0.19$).

The simulation was able to predict female orientation in the RP1 experiment (Fig. 3C vs Fig. 3A, $\chi^2=6.26$, d.f.=4, $P=0.18$) with high overlap between the frequency ranges predicted by the simulation and bootstrapped real data (Fig. 3E). Path vectors were also similar (Fig. 3C inset vs Fig. 3A inset, $\chi^2=2.83$, $P=0.24$). The simulation was, however, not able to entirely capture female orientation behaviour in RP2 (Fig. 3D vs Fig. 3B, $\chi^2=13.35$, d.f.=4, $P<0.01$). In this case, real females approached the nearest and loudest speakers

(C and D) in equal numbers whereas most females in the simulation approached the loudest speaker (D). The frequency ranges produced by the simulation did show overlap with the bootstrapped data, albeit to a lesser extent (Fig. 3F). The path vectors, however, were not significantly different between a run of the simulation and the real paths (Fig. 3D inset vs Fig. 3B inset, $\chi^2=0.14$, $P=0.93$).

DISCUSSION

The simulation successfully predicted both female acoustic orientation behaviour at the population level and the forms of phonotactic paths, suggesting that our model of the mechanisms underlying cricket phonotaxis can recapture phonotaxis behaviour in complex real-world environments. The simulation was built using data from phonotaxis in ideal acoustic conditions with only two active sources (Mhatre and Balakrishnan, 2007). It was, nonetheless, able to recapture acoustic orientation behaviour under multi-source conditions in the field when the empirically measured characteristics of outdoor sound transmission were incorporated in the model. The discrepancy between the simulated and real female preferences in one of the experiments (RP2) might be explained by visually mediated attraction towards the less loud but closer speaker, which would be visible under ambient light conditions in the field. This speculation is supported by the observation in the two-speaker experiment that a few females were attracted to a silent speaker (Mhatre and Balakrishnan, 2007). Female crickets modulate their preferences for song based on visual input, sometimes becoming more selective under high light conditions (Stout et al., 1987; Weber et al., 1987). Female cricket phonotaxis is also known to be modulated by their perception of predation risk as judged by the lack of cover under which to hide (Hedrick and Dill, 1993). In the present study, females were tested in areas with almost no cover and might have approached closer speakers in an attempt to reduce predation risk.

Our experiments with real females show that the ability to track and locate the loudest speaker is reduced with an increasing number of sources, a result similar to that obtained in a study with painted reed frogs (Bishop et al., 1995). We found that this ability also depends on the starting position although, interestingly, only negligibly on initial orientation. There was also no consistent female orientation towards the loudest source in a chorus. Both of these observations were also supported by the results of the simulation. Female orientation changed based on SPL at initial position and on distance of the initial position relative to the sound sources, and was not easy to dissect using conventional statistical methods. Our results suggest that physiology-based simulation models may offer a more powerful alternative to conventional statistical methods for predicting orientation and localization behaviour in complex, real-world environments.

The experiments and the simulations both predict that female crickets in dense, multi-male choruses are not always likely to locate the loudest male. If they do choose the loudest males as mates, which has been implied from the higher capture rate observed in pitfall trap experiments (Forrest and Green, 1991; Farris et al., 1997), results from the present study indicate that this cannot result from the sound localization mechanism alone but must involve strategies for sampling multiple males. The simulation model is a useful tool for deciphering the components of female choice that are a consequence of the sound localization mechanism alone. Similarly, it can be used to isolate the acoustic component of multimodal orientation behaviour.

Further elaboration of the model is required to capture the full complexity of cricket phonotaxis behaviour. Incorporation of

multimodal information and female preferences for different song features could improve its predictive power. Nonetheless, we believe that this simulation model represents a significant step towards predicting orientation and localization in complex acoustic environments.

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