ANIMAL BEHAVIOUR, 2008, **76**, 723–735
doi:10.1016/j.anbehav.2008.04.015

Leaders and followers in katydid choruses in the field: call intensity, spacing and consistency

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*(Received 3 December 2007; initial acceptance 13 February 2008;
final acceptance 21 April 2008; published online 17 June 2008; MS. number: D-07-20004)*

Synchrony is a phenomenon that is seen in several rhythmically signalling animals including fireflies, fiddler crabs (visual synchrony), frogs and katydids (acoustic synchrony). During acoustic interactions in katydids, synchrony is, however, imperfect and synchronous chirps typically lead or follow each other. In some katydid species, females have a strong preference for leading chirps, suggesting that consistent follower males would be at a disadvantage unless they used alternative strategies to attract females. In the katydid species *Mecopoda* 'Chirper' we used chirp period measurements to investigate whether individual males were consistent leaders and followers and whether followers could use three potentially advantageous strategies in field choruses: calling louder than leading males; spacing themselves such that they were either louder than leading males or were perceived to lead the leading males in some part of their acoustic range; and calling when leading males were silent. During acoustic interactions in choruses, three-fifths of the followers called more often when leaders were not calling. Leaders were, however, typically louder than followers but spacing enabled some quieter males to gain areas where they were the loudest among all males in a chorus. Chirp period and thus lead probability of males had low repeatability with no consistent leaders and followers across nights. Thus the disadvantage of being a follower in katydid choruses on a particular night could potentially be offset by solo calling or by the follower being a leader on other nights.

Keywords: chorus; katydid; *Mecopoda*; spacing; synchrony

Males of many species of frogs and insects use acoustic signals to attract potential mates over long distances (Alexander 1967; Gerhardt 1994). In some species, multiple individuals call in aggregations termed choruses (Greenfield 1994). Chorusing behaviour often involves very precise timing relationships between the chirps of neighbouring males, with some species displaying synchrony (large overlap of chirps) or alternation (no overlap of chirps) or both (Sismondo 1990; Greenfield 1994; Grafe 1996). Where synchrony occurs, it is often imperfect and the chirps of calling males lead or lag behind each other. Females of many synchronizing species of frogs and katydids prefer leading calls (Dyson & Passmore 1988; Greenfield & Roizen 1993; Grafe 1996; Snedden & Greenfield 1998; Gerhardt & Huber 2002; Fertschai et al. 2007). Greenfield et al. (1997) and Greenfield & Roizen (1993) suggested that female preference for leading calls has driven the evolution of synchronous chirping in katydid choruses. They proposed that males may increase their attractiveness to females by synchronizing with the calls of their neighbours and leading them by a small amount of time.

In katydid species such as *Neoconocephalus spiza*, where synchrony is achieved by inhibitory resetting (Greenfield et al. 1997), interacting males lead and follow on every alternate chirp (Greenfield & Roizen 1993), so that the males have approximately equal advantage in terms of lead. In species such as *Mecopoda elongata* and *Mecopoda* 'Chirper', however, the mechanism underlying synchrony differs from inhibitory resetting. In these species, the male with the faster intrinsic chirp rate can lead the majority of the other male's chirps (Hartbauer et al. 2005; Nityananda & Balakrishnan 2007). Since females approach leading calls in laboratory phonotaxis experiments in *M. elongata* (Fertschai et al. 2007), males that consistently manage to produce leading chirps would be expected to have much greater mating success than males that do not. In natural

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0003−3472/08/$34.00/0

choruses in the field, this advantage of leading might, however, not be as great if followers managed to compensate for their disadvantage through different strategies. Alternatively, if there were no consistent leaders, followers on one night might offset their disadvantage by being leaders on another night and the advantage of leading might be similar across animals through a season. We investigated both these possibilities by examining the calls of males in choruses in the field.

In the first case, followers may have different strategies to compensate for the female preference for leading chirps. For instance, followers could have calls that were attractive enough in other features to overcome the preference for leading chirps. Numerous studies have examined the relative attractiveness of male call features in controlled laboratory-based studies on katydids (Greenfield & Roizen 1993; Snedden & Greenfield 1998; Berg & Greenfield 2005; Fertschai et al. 2007). None of these studies, however, examined actual calling males with natural spacing in the field and related their call intensities to the disadvantages caused by call timing.

A follower could also avoid direct competition by calling more often when the leader is silent. A few studies (Minckley et al. 1995; Greenfield & Snedden 2003) have examined call timing in choruses in the field in the context of selective attention. These field studies did not, however, examine the timing of calls and call bouts as possible strategies within a chorus.

One more feature that a follower could use to gain advantage is spacing. Sound transmission delays would change the timing relationships between chirps so that by strategic spacing, followers at source could gain areas where their calls were leading. Spacing could also enable followers to gain areas where their calls were louder. A few studies have examined the advantage that spacing may confer on calling males in the field (Forrest & Green 1991; Arak & Eiriksson 1992; Farris et al. 1997) but not in relation to call timing.

To evaluate potential advantages that males might have in the field, one needs to know both how males call in the field and what the preferences of females are for different call features. We investigated the former in the species *M.* ‘Chirper’ (described in Nityananda & Balakrishnan 2006). As female preferences are currently unknown for this species, we asked whether followers could have any advantages given the features of their calling songs. For example, if one found that followers were never louder than leaders, then this would rule out the possibility that they could overcome their disadvantage because they were louder.

Leaders would also not have as great an advantage if lead was not consistent across nights. Males would then have variable mating success across nights and perhaps similar mating success over a breeding season. While the repeatability of various other ensiferan call features (chirp period, chirp duration) has been investigated in the field (Butlin & Hewitt 1986; Hedrick 1988), to the best of our knowledge, no field study has examined the consistency of lead in natural habitats.

Previous studies of this species have shown that chirp rate is a predictor of lead probability during acoustic interactions with other males. Furthermore, males have a solo intrinsic chirp period that differs from their duet chirp period because of adjustments made during interactions with other males (Nityananda & Balakrishnan 2007) and the male with the faster intrinsic chirp rate leads more than 50% of the partner’s chirps (Nityananda & Balakrishnan 2007). This is, however, true in only 75% of pairwise interactions, since males can change their intrinsic periods during interactions (Nityananda & Balakrishnan 2007). The change in intrinsic period is separate from the change caused by chirp-by-chirp adjustments, although both occur in response to external chirps (Nityananda & Balakrishnan 2007). The changed intrinsic period is a better predictor of lead probability than the solo intrinsic chirp period and we used it to investigate the consistency of lead in the field. The lead probability for a male is, however, also determined by the chirp period values of the other males calling on a night and the chirp period of the male’s nearest neighbour. We therefore asked three questions. (1) Is the chirp period of a male consistent across nights? (2) Is the chirp period of a male relative to those of other males calling on a night consistent across nights? (3) Is the chirp period of a male relative to his nearest neighbour consistent across nights?

METHODS

We carried out the study in an area of natural vegetation (approximate dimensions: 180 × 300 m) during the breeding season of *M.* ‘Chirper’ (August to October) in 2004 and 2005. Individuals of this species are commonly found in habitat that consists of tall grasses and some low bushes. They call in choruses of three to six males spanning an area of approximately 18 m^2. The individuals in the choruses can sometimes be spaced wide enough apart that some of them are not heard by other individuals of the same chorus (Nityananda et al. 2007). Males call from 1830 to 2130 hours at heights ranging from 0 to approximately 1 m above the ground. We carried out all recordings and measurements during the peak calling time for the species.

Chorus Recordings in the Field

We located males calling in choruses and noted their positions. A chorus was defined as a group of calling males such that no two males were separated by more than 10 m. On another night, we recreated the choruses by placing males in nylon mesh cages (approximate dimensions: 15 × 8 cm and 8 cm high) at the exact positions from which the males had been calling. In most cases, the males that were placed in cages were the males that had been calling from the same spot the night before. In some cases, where these particular males did not call or were no longer available, other males were used in their place. We placed tiepin microphones with custom-built preamplifiers in front of each of the cages and digitized their output at a sampling rate of 16 kHz onto a laptop computer (IBM type 1830) using a Measurement Computing (Measurement Computing Corp., Norton, MA, U.S.A.) DAS16/330 A/D card. The input from each male was recorded via a separate channel using the software

Labview 6.0 (National Instruments, Austin, TX, U.S.A.). We processed the acquired calls using the software MatLab (Mathworks, Natick, MA, U.S.A.) and determined the times of onsets and offsets of the calls using a custom-built program (C. Sekhar, ECE, Indian Institute of Science, Bangalore, India). We performed further analysis on the chirp onsets using custom-built MatLab programs to determine the number of chirps of a male that did not overlap with those of any other male (solo chirps) and the number of chirps of a male that overlapped and led the chirps of each of the other males in a chorus. The total number of choruses was nine. The mean duration of recordings across all nine choruses ± SD was 25.3 ± 12.7 min.

Sound Pressure Level and Attenuation Measurements

We measured the sound pressure level (SPL) of the calls of individual males in the field at 30 cm from source using a CEL (CEL, Bedford, U.K.) 414 Precision Impulse Sound Level Meter with a Larson Davis (Larson Davis, Inc., New York, U.S.A.) 2540 microphone (frequency range 32 Hz–40 kHz). Ten readings were taken for each male using the 'Peak Hold' setting and the average taken as the SPL of that male's call. We calibrated the SPL values of the CEL 414 Precision Impulse Sound Level Meter against a Brüel & Kjaer (Brüel & Kjaer, Naerum, Denmark) Sound Level Meter 2231 with a ¼ ″ microphone (4939, frequency range 4 Hz–70 kHz) and corrected all SPL values measured using this calibration. We performed this correction so that the measurements would be comparable to those of previous publications. For the purposes of this study, however, this correction was unnecessary since the main focus of the study was on relative values of SPL rather than absolute values.

We randomly chose one of the males in the chorus as the focal male. We determined the attenuation of the call in the habitat by broadcasting chirps of an individual of the same species from the position of the relevant male at the SPL at which the male had been calling, or by placing another male at that position and measuring the difference between the SPL 30 cm from source and the focal male's position. We broadcast chirps in the field using a laptop computer (IBM Type 1830) and replayed previously recorded chirps through a National Instruments NI-DAQ 6715 D/A card, an Avisoft amplifier and an Ultrasonic Scanspeak (Avisoft Bioacoustics, Berlin, Germany) speaker (frequency range 1–120 kHz). The chirps broadcast had previously been recorded with a Brüel & Kjaer Sound Level Meter 2231 with a ¼ ″ microphone (4939, frequency range 4 Hz–70 kHz) and digitized at a sampling rate of 200 kHz using a National Instruments NI-DAQ AT--MIO-16E-2 card and the software Labview 6.0. We combined attenuation data from all choruses to generate an attenuation curve for the habitat and fitted a curve to the data using the curve-fitting toolbox of MatLab.

Song Recording and Analysis

To examine whether there are consistent leader or follower males, we investigated the chirp periods of calling males of *M.* 'Chirper' in the field. We located calling males in the field on 4 consecutive nights and marked each male on the pronotum with nontoxic paint markers (Edding 780, Edding, St Albans, U.K.). Each male was given a unique three- or four-colour code. We marked 102 males over 4 nights.

We initiated recordings of calling males 4 days after the last night of marking. We identified focal calling males in the field and noted their identities. We silenced the neighbours of the males by disturbing them when they called, and recorded the calls of the focal males using Sony (Minato, Tokyo, Japan) WM-D6C Professional Walkman cassette recorders and either a Sennheiser (Wennebostel, Germany) MKH20 P48 microphone (frequency range 20 Hz–20 kHz) or a Sony ECM-MS957 microphone (frequency range 50 Hz–18 kHz). We located and identified the nearest neighbours of the focal males and recorded their calls as above after silencing males calling in the vicinity. After each recording, we measured the ambient temperature with a Kestrel (Sylvan Lake, U.S.A.) 3000 Pocket Weather Station. The recordings were made over 12 nights in August 2005 at the peak of the breeding season.

We digitized the recorded calls using a Creative Sound Blaster A/D card at a sampling rate of 44.1 kHz. We analysed the digitized calls using the software MatLab and determined the times of onsets and offsets of the chirps using a custom-written program (C. Sekhar, ECE, Indian Institute of Science). We calculated the chirp period of each male using custom-written MatLab programs. The mean number of chirps analysed per animal ± SD was 157.5 ± 78.4.

Data Analysis

Chorus recordings in the field

To examine calling patterns on a global scale across all males, we analysed three features that could potentially provide advantage to a male in a chorus. These were the number of leading chirps, the number of chirps that did not overlap with any other male's chirps (solo chirps) and the male's SPL at 30 cm. We normalized the first two by dividing them by the total time of the recording bout to obtain the corresponding frequency. We carried out pairwise linear correlations between the three features across all choruses. To examine calling patterns at a more local scale, we also examined the values of the features relative to each male's nearest neighbour and carried out pairwise linear correlations between these relative values of the three features across all choruses.

We investigated whether males who had a lower number of leading chirps relative to their nearest neighbours compensated either by having a greater number of solo chirps or a greater SPL at source relative to their nearest neighbours. Using chi-square tests ($\alpha = 0.05$) we examined whether the observed proportions of follower males who had a greater relative number of solo chirps or a greater relative SPL were different from the proportions expected if followers did not manage to compensate for their disadvantage at all, that is, no followers had greater values for either of these two features. Thus, if the null hypothesis was rejected, it would imply that some proportion of followers managed to compensate for their disadvantage. If the relative number of leading chirps (number of leading chirps of focal male – number of leading chirps of the nearest neighbour) or solo chirps (number of solo chirps of focal male – number of solo chirps of the nearest neighbour) between two males was less than 50, the males were assumed to be equally attractive. Similarly, males that had SPL values within 2 dB of each other were assumed to be equally attractive. Studies on both crickets (Hedwig & Poulet 2005) and bushcrickets (Römer et al. 1998) indicate that females can distinguish between signals that differ by 2 dB and we therefore chose this as the minimum possible intensity difference by which one chirp could be more attractive than another.

We also examined the patterns of allocation of calling effort put into leading chirps, solo chirps and SPL in each individual to identify broad strategies that males might follow in the field. Towards this purpose, we classified each male as having a value greater than (coded as g), lower than (coded as l) or equal to (coded as e) his nearest neighbour for each of the three features. The combined code across the three features was taken to represent the 'strategy' a male was using. Thus, a strategy 'gge' would mean that the male had a greater number of leading chirps and solo chirps than his nearest neighbour but had equal SPL. We examined which of these 'strategies' were most common across all males sampled.

Spacing measurements and simulations

The effect of spacing on sound pressure level. The spacing of males in a chorus affects the area in which a male is louder than his neighbours (Römer & Bailey 1986; Arak & Eiriksson 1992). Because of the effect of attenuation, the perceived intensities of male calls depend on the position of the receiver relative to all the males in the chorus. To examine the effect of spacing on intensity, we noted the positions of calling males in each chorus and mapped them using the software MAPINFO Version 5 (MapInfo Corporation, Berkshire, U.K.). We then used the mapped positions in a simulation performed in MatLab using custom-written programs. Using the simulation, we calculated and plotted the areas within a male's acoustic range in which he had a greater SPL than all the other males in the chorus. These areas were calculated based on the sound attenuation curve obtained from field recordings and assuming a female phonotactic threshold of 58 dB SPL. A grid was made of the area in which the males were audible, with squares of 100 cm^2 each. The SPL of each male at the centre of each square was determined by calculating the distance to the centres and then using the attenuation curve to find the reduced SPL of the male at that distance. While the broadcast areas of calling bushcrickets could be biased in particular directions (Römer & Bailey 1986), our observations of calling males indicated that males move and change their direction while calling. Since the cages in which males were placed allowed them to move as they would when uncaged, for the purpose of this simulation, we assumed that males broadcast with equal intensity in all directions. Whenever a male had an SPL within 2 dB of the loudest male, it was assumed that both males were equally loud. The area in which a male had an SPL greater than or equal to that of the other males ('loudest area') was calculated (in cm^2) by multiplying the number of squares in which the SPL was greater or equal by 100. We compared the relative areas in which each male had an advantage with the relative SPLs at source to see whether spacing conferred an extra advantage to the male. We compared the mean loudest areas of followers and leaders using a Student's two-tailed t test ($\alpha = 0.05$). In addition, we performed a multiple regression to investigate the effect of three variables on the loudest area: distance to the loudest male; SPL relative to the loudest male; and absolute SPL. The loudest males were not used for this analysis.

The effect of spacing on the number of leading chirps. Since acoustic transmission delays are approximately 3 ms/m (assuming the speed of sound to be 345.1 m/s, 1 m would cause a delay of $1/345.1 = 0.0029$ s), spacing would also affect what a female at various positions in the area around a male would perceive as a leading or a following chirp. Thus, the number of leading and following chirps for a male relative to his neighbour's chirps would vary from point to point in the field. To examine the effect of spacing on the perceived number of leading chirps, we noted the positions of calling males in the choruses and mapped them using the software MAPINFO Version 5. We then used the mapped positions in a simulation that calculated and plotted the areas within a male's acoustic range in which he had a greater number of leading chirps than his nearest neighbour. The simulation was similar to the one used above except that each square in the grid had an area of 1 m^2. Whenever a male led another male by 50 chirps or less, it was assumed that both males were equally attractive. We correlated the area in which a male had a greater number of leading chirps than his nearest neighbour with the relative number of lead chirps at source to see whether males who were followers at source had some area in which they led their nearest neighbours.

Chirp period recording in the field

We performed a two-way ANOVA to determine whether there was a significant difference in chirp period caused by male identity and temperature. To determine whether the chirp periods of males were similar on different nights, we first carried out a linear regression of chirp period against temperature for every male. Wherever the regressions were significant, the values were corrected to a temperature of 24 °C, the modal temperature. We then tested these corrected values for repeatability using the formula (Lessels & Boag 1987):

$$r = s_A^2/(s^2 + s_A^2)$$

where r is repeatability, s_A^2 is the between-groups variance component and s^2 is the within-groups variance component derived from a one-way analysis of variance. Only males who were recorded on 3 or more nights were used for this analysis.

To determine whether the chirp period of a male remains the same relative to all other males calling on a particular night, we calculated the mean period across males for each night and determined the deviation of each male's period from this mean for each night. The deviation represents the male's position in the distribution of periods of males calling on that night. We calculated the repeatability of this deviation.

To determine whether a male maintains a constant period difference with his nearest neighbour across nights, we calculated the period of each male relative to his nearest neighbour for each night on which the male called by subtracting the chirp period of the male from that of his nearest neighbour. We calculated the repeatability of this relative period across nights.

For all statistical analyses we used the software Statistica (Statsoft, Inc., OK, U.S.A.) or the Analysis ToolPak of Microsoft Excel (Microsoft Corp., Seattle, WA, U.S.A.).

RESULTS

Choruses in the Field

Call timing and intensity

The number of males in a chorus ranged from three to six. The mean SPL (peak) of the call at 30 cm ± SD was 91.5 ± 5.5 dB ($N = 29$ males). Different choruses had various ranges of SPLs with some choruses having males with SPLs only 2 dB apart while others had as much as a 26 dB difference between the loudest and quietest male in the chorus (Table 1). The average difference between the loudest and quietest males in a chorus ± SD was 8.3 ± 7.18 dB. The average number of leading chirps produced per min by males across all choruses ± SD was 44.4 ± 39.0. This number was variable both within and across choruses. The number of solo chirps was considerably lower than the number of leading chirps, with the average number per min ± SD being 13.3 ± 16.1.

On a global scale, at the level of the population and across choruses, none of the three features examined, that is, number of solo chirps, number of leading chirps and SPL, were significantly correlated with each other (Pearson correlation: leading chirps and SPL: $r_{27} = 0.156$, $P = 0.419$; solo chirps and SPL: $r_{27} = 0.14$, $P = 0.469$; solo chirps and leading chirps: $r_{27} = -0.269$, $P = 0.158$; Fig. 1a–c). No male had high values for all three features.

Examining the values of the features of the males on a local scale relative to their nearest neighbours, however, revealed some interesting patterns. Relative SPL was significantly positively correlated with the relative number of leading chirps ($r_8 = 0.674$, $P = 0.033$; Fig. 2a) but not with the relative number of solo chirps ($r_8 = -0.119$, $P = 0.742$; Fig. 2b). The relative number of solo chirps was also not correlated with the relative number of leading chirps ($r_8 = -0.018$, $P = 0.961$; Fig. 2c).

Do followers produce louder chirps at source or more solo chirps than neighbouring leaders?

Nine of the 24 males for which all relative values of the three features were measured had a lower number of leading chirps per min relative to their nearest neighbours (Table 2, column 2, bold face). Five of these 'followers' (56%) had a greater number of solo chirps per min (Table 2, column 4, bold face italicized) relative to their respective nearest neighbours and none of them had a greater SPL (Table 2, column 5). The proportion of followers with a greater relative number of solo chirps was significantly different from the proportion expected if all followers failed to compensate for their disadvantage ($\chi^2_1 = 18$, $P < 0.001$).

Table 1. Source sound pressure level (SPL) and acoustic range areas of calling males in a chorus and areas in which a male was the loudest in a chorus

Chorus number	Male identity	SPL 30 cm from source (dB)	Active range area (m^2)	Loudest area (m^2)
1	a	92.9	1399.8	484.40
1	**b**	92.1	1181.8	**52.90**
1	**c**	85.1	276.0	**1.30**
1	e	93.7	1657.9	1617.20
2	a	98.7	4572.7	4551.20
2	d	90.9	914.6	21.20
2	f	89.0	622.7	1.16
3	**a**	90.6	859.5	**10.96**
3	c	96.3	2802.3	2729.00
3	d	89.6	705.0	364.60
4	a	86.3	354.1	268.79
4	**b**	83.0	180.9	**65.81**
4	c	83.9	215.3	135.93
5	**a**	95.0	2142.0	**0.00**
5	b	86.0	332.0	0.00
5	c	112.0	72 401.0	72 401.00
6	a	89.7	716.7	106.80
6	**b**	95.1	2195.9	**1374.10**
6	**c**	86.1	342.1	**31.80**
6	d	94.2	1812.2	1181.90
7	a	89.7	722.6	251.81
7	b	91.5	1032.8	760.12
7	**c**	91.3	1007.9	**735.49**
8	a	92.5	1272.7	**1084.70**
8	b	88.5	565.6	205.95
8	c	88.6	573.4	45.39
9	a	97.0	3229.6	2881.50
9	**b**	92.2	1202.7	**7.71**
9	c	91.3	1004.8	567.47

Each row represents one male. Bold face represents follower males. Only males for which SPL measurements were made were used in this analysis.

The most common 'strategies' seen across choruses were 'lgl', 'glg', 'lle' and 'gge' (Fig. 3). Males with the 'lgl' strategy had a greater number of solo chirps but a lower number of leading chirps and SPL relative to their nearest neighbours. Males with the 'glg' strategy had a lower number of solo chirps but a greater number of leading chirps and SPL relative to their nearest neighbours. These complementary strategies were commonly seen when two males were each other's nearest neighbours. The strategies 'gge' and 'lle' were also common complementary strategies. In these two, males had equal SPL but, in the first, males had a greater number of solo and leading chirps, whereas in the second, males had a lower number of solo and leading chirps. No males had a strategy of 'ggg', that is, no male had greater values for all three features relative to his nearest neighbour.

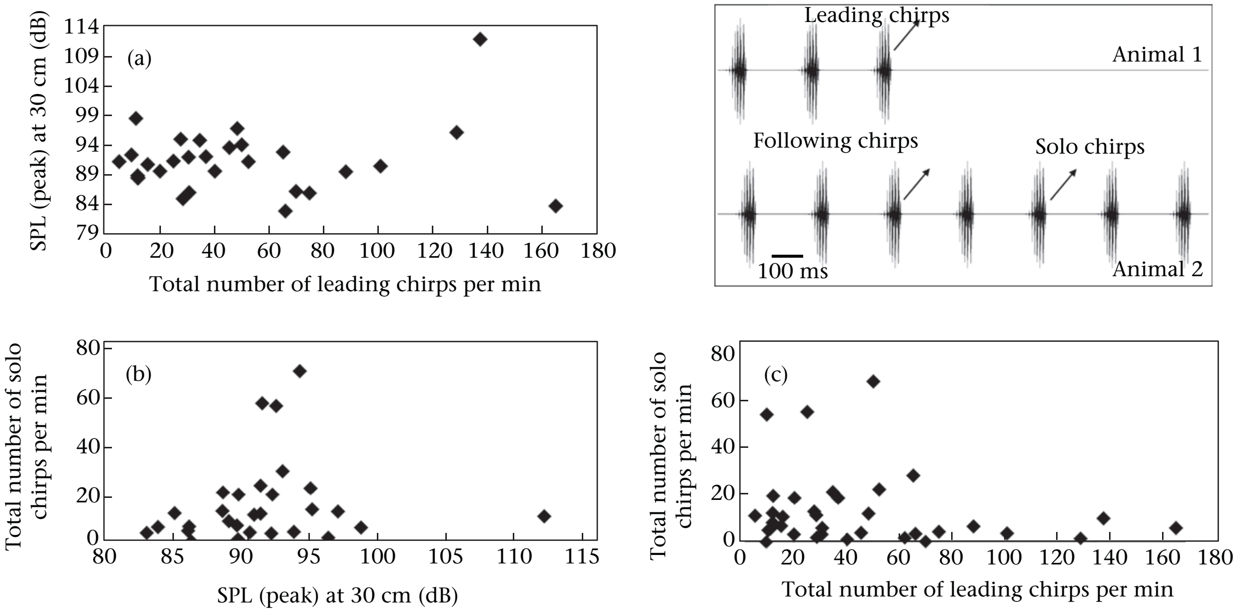

Figure 1. Relations of three call features of males calling in the field. (a) Sound pressure level (SPL) at 30 cm in relation to the total number of leading chirps per min. (b) Total number of solo chirps per min in relation to the SPL at 30 cm. (c) Total number of solo chirps per min in relation to the total number of leading chirps per min. The inset depicts a representation of the chirping pattern of *Mecopoda* 'Chirper' demonstrating leading, following and solo chirps.

Spacing and attenuation

The average nearest-neighbour distance over 36 males ± SD was 3.99 ± 2.32 m and ranged from 0.67 to 13.38 m. Figure 4 shows the attenuation curve of the call with distance in the habitat. The attenuation followed a power law ($Y = 13.21 \times X^{0.277}$, $r^2 = 0.56$) and increased dramatically for changes in distance close to the male but did not increase as much for similar changes much further from the animal. The attenuation curve did not, however, saturate even at a distance of 14 m.

The effect of spacing on sound pressure level

The area in which a male was loudest or within 2 dB of ('equal to') the loudest male ('loudest area') was significantly positively correlated with the SPL of the call at source ($r_{27} = 0.75$, $P < 0.0001$; Fig. 5). There was an exponential relationship ($Y = 3.815 \times 10^{-8} \times e^{0.252x}$, $r^2 = 0.998$) between the loudest area and the SPL at source. Males with low SPLs at source had a much lower loudest area than males with higher SPL values. This was especially noticeable below 91 dB SPL. Within a chorus, the loudest male always had the largest area in which he was the loudest (Table 1). Multiple regression using males other than the loudest males in a chorus showed a significant effect of SPL relative to the loudest male on the loudest area ($\beta = 0.553$, $P = 0.021$). There was no significant effect of the distance to the loudest male and the absolute SPL on the loudest area (distance to the loudest male: $\beta = 0.4$, $P = 0.065$; absolute SPL: $\beta = 0.359$, $P = 0.092$).

Males with SPLs much lower than the loudest male did not have large loudest areas when they were either close to the loudest male (Fig. 6a, male 3) or further away (Fig. 6b, male 3). Males with SPLs closer to that of the loudest male in a chorus, however, had greater loudest areas both when they were close to the loudest male (Fig. 6c, male 4) and further away (Fig. 6d, male 3). Loudest areas were not significantly different between followers and leaders (Student's *t* test: $t_{16} = 0.93$, $P = 0.362$). In all, eight of 10 followers (80%) had a large or moderate loudest area because of a combination of call intensity and spacing (Table 1, column 5).

The effect of spacing on the number of leading chirps

Across all choruses, the number of leading chirps at source relative to the nearest neighbour was significantly positively correlated with the area in which a male was perceived to be a leader ($r_{27} = 0.515$, $P = 0.004$). The significance of the correlation coefficients within each individual chorus could not be established because of the low number of individuals (samples) in each chorus. In three of the choruses, however, the male with the largest number of leading chirps relative to his nearest neighbour did not have the largest area in which he led the nearest neighbour by more than 50 chirps (Fig. 7: choruses 3, 6 and 7).

Males with the lowest number of leading chirps at source had the smallest areas in which they led their nearest neighbours, with one exception (chorus 4). None of the followers had areas in which they led their nearest neighbours (negative values on the *X* axis, Fig. 7).

Consistency of Chirp Period

A total of 44 males were recorded over 12 nights. Twenty-one of these males were recorded on 3 or more nights. The chirp periods across nights for these males are

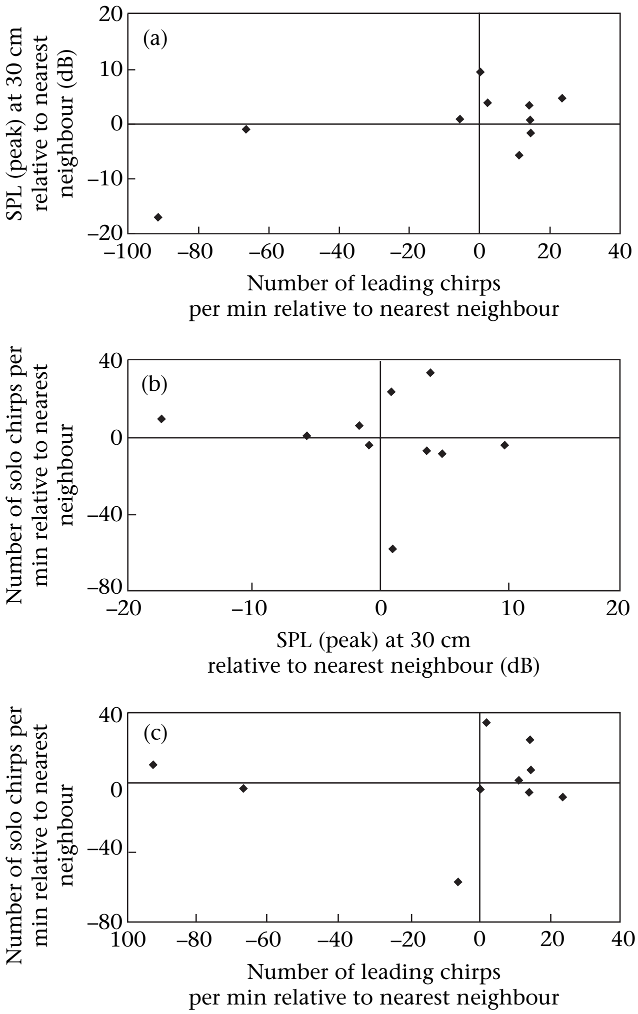

Figure 2. Relations of three call features of males relative to those of their nearest neighbours. (a) Sound pressure level (SPL) at 30 cm relative to the nearest neighbour in relation to the total number of leading chirps relative to the nearest neighbour. (b) Number of solo chirps per min relative to the nearest neighbour in relation to the SPL at 30 cm relative to the nearest neighbour. (c) Number of solo chirps per min relative to the nearest neighbour in relation to the total number of leading chirps relative to the nearest neighbour.

given in Table 3. On no two nights did a male have the same nearest neighbour.

We found chirp period to be normally distributed (Kolmogorov−Smirnov test: $P > 0.2$). Both male identity and temperature had a significant effect on the chirp period of males (two-way ANOVA: identity: $F_{19,23} = 2.508$, $P = 0.019$; temperature: $F_{4,23} = 20.307$, $P < 0.001$). We could not determine whether there was an interaction effect between temperature and identity because the sample sizes in some of the temperature classes were too small. Testing for homogeneity of variance revealed no significant difference between the variances of the groups (Bartlett's $\chi^2_{17} = 13.87$, $P = 0.68$). The temperature within a night varied only within 2 degrees on all except 1 night (Table 3). The variation in period on a particular night was therefore caused by male identity.

Table 2. Values of three features of the calls of chorusing males relative to those of their nearest neighbours

Chorus number	Male identity	Relative no. of leading chirps per min	Relative no. of solo chirps per min	Relative SPL (dB)
1	a	13.9	25.3	0.8
1	**b**	**−13.9**	**−25.3**	**−0.8**
1	**c**	**−7.6**	***8.3***	**−7.0**
1	d	−0.4	−8.3	
1	e	4.8	2.2	
1	f	−4.8	−2.2	
2	a	−0.1	−2.5	9.7
2	b	−0.2	−1.8	
2	c	−0.1	1.9	
2	d	0.1	4.4	
2	e	−2.1	−3.1	
2	f	2.1	3.1	
3	**a**	**−27.8**	***2.2***	**−5.7**
3	b	−11.7	−5.0	
3	c	27.8	−2.2	5.7
3	d	11.7	5.0	
4	a	−1.9	−6.2	
4	**b**	**−66.8**	**−2.5**	**−0.8**
4	c	66.8	2.5	0.8
5	**a**	**−92.1**	***11.4***	**−17.0**
5	b	4.4	−5.8	−26.0
5	c	92.1	−11.4	17.0
6	a	13.7	−5.1	3.6
6	**b**	**−6.1**	**−56.1**	**0.9**
6	**c**	**−13.7**	***5.1***	**−3.6**
6	d	6.1	56.1	−0.9
7	a	14.3	7.8	−1.6
7	b	10.4	44.7	0.1
7	**c**	**−14.3**	**−7.8**	**1.6**
8	a	2.0	34.9	3.9
8	b	−3.6	−7.6	−0.1
8	c	−2.0	−34.9	−3.9
9	a	23.2	−7.0	4.8
9	**b**	**−23.2**	***7.0***	**−4.8**
9	c	19.3	10.6	−5.7

Each row represents one male. Bold face represents follower males. Italics represent follower males with higher relative values of other features. Relative sound pressure level (SPL) was calculated when the SPLs of both the male and the nearest neighbour were known.

The repeatability of the chirp period of males was low and not significant ($r = -0.117$, $F_{19,60} = 0.903$, $P = 0.58$). Deviation from the mean period in one night also had low repeatability ($r = 0.167$, $F_{20,64} = 1.809$, $P = 0.04$). The repeatability value for the period of males relative to their nearest neighbours was also low ($r = 0.163$, $F_{8,19} = 2.545$, $P = 0.045$). In most cases, males that were slower than their nearest neighbours on one night were faster on other nights.

DISCUSSION

Potential Strategies of Followers in Choruses within a Night

Within a night, followers in a chorus might follow different strategies to compensate for their disadvantage. Females in other species that show a marked preference

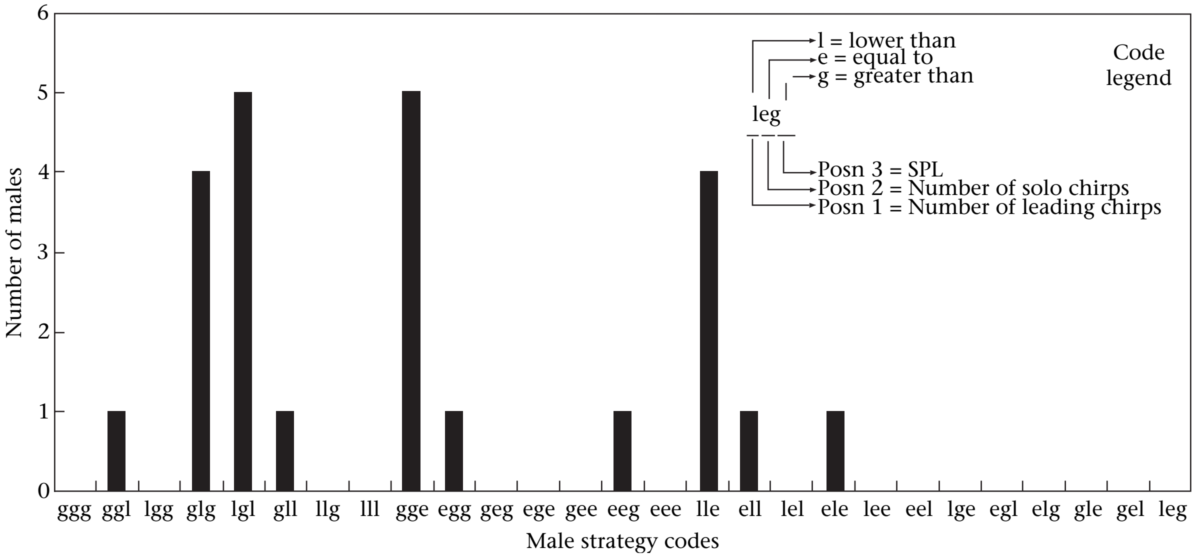

Figure 3. Frequency histogram of 'strategies' of males in choruses in the field. 'g' denotes a greater value than, 'l' a lower value than, and 'e' a similar value to, the nearest neighbour. The first position in the code for the strategy refers to the relative number of leading chirps, the second to the relative number of solo chirps and the third to the relative sound pressure level. See text for details.

for leading chirps (reviewed in Gerhardt & Huber 2002) are influenced by other traits as well (Greenfield & Roizen 1993; Berg & Greenfield 2005; Fertschai et al. 2007) and followers could, in principle, make use of these traits in the field to overcome their disadvantage.

Are followers louder than leaders?

Behavioural studies by Snedden & Greenfield (1998) on *N. spiza* show that the advantage that lead gives a male can be offset by greater intensity of the following chirps. In a behavioural study that used artificially spaced males in an outdoor arena, Berg & Greenfield (2005) found that call power explained female choice better than call timing. Females of the species *M. elongata* were also seen to prefer following males if these were sufficiently louder (Fertschai et al. 2007). A male could thus offset the disadvantage of being a follower by calling more loudly (Snedden & Greenfield 1998; Römer et al. 2002).

Our results from *M.* 'Chirper' in choruses in the field indicate, however, that leading males are likely to be louder than their nearest neighbours. Thus, followers in a chorus do not compensate for their disadvantage by being louder than leaders. Fertschai et al. (2007) showed that given equal call intensities, followers would attract a greater percentage of females than predicted by lead alone if females are randomly spaced in the field. However, given that leaders are likely to be louder males, and that the loudest male at source is invariably the male with the greatest area in which he appears loudest, the area in which a following male is attractive would be less than they predicted.

Do followers have more solo chirps than leaders?

Another strategy that followers could use is calling during the silent bouts of leaders. Several studies have shown that males modify their calling at different

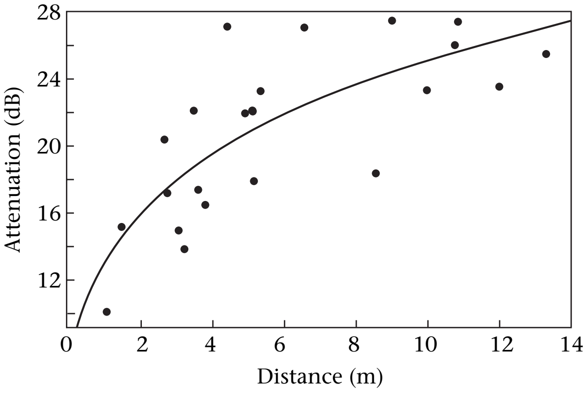

Figure 4. Attenuation of *Mecopoda* 'Chirper' calls in the field.

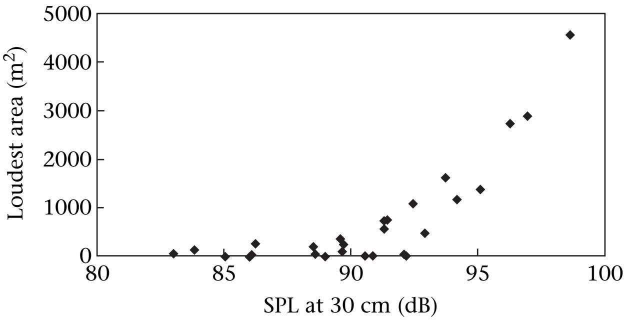

Figure 5. Areas in which males were the loudest in relation to their sound pressure level (SPL) 30 cm from source. One male (SPL = 112.02 dB, loudest area = 72 401 m^2) was excluded to enable scaling that allowed clear representation of the other males in the figure.

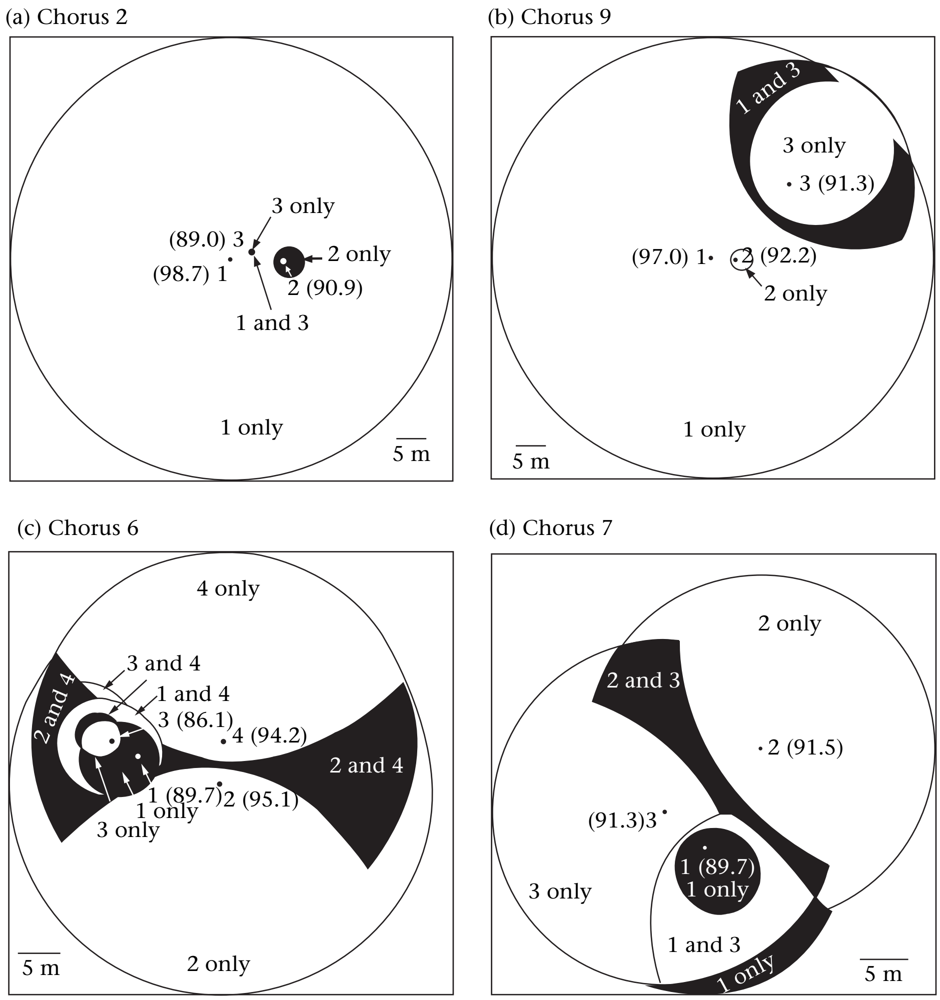

Figure 6. Four choruses (a–d), each showing the areas in which individual males were the loudest. Positions of the males are indicated by points. Different areas of black or white represent areas in which different males were the loudest. Labels indicate which male or males were loudest in a particular area. Sound pressure levels at 30 cm are given within parentheses.

timescales in the presence of acoustic competition (Samways 1977; Latimer 1981; Latimer & Broughton 1984; Römer et al. 1989). Katydids can restrict the time slot in which they call in the presence of competing species (Samways 1977; Römer et al. 1989).

In *M.* 'Chirper' a significant proportion of followers had a greater number of solo chirps relative to neighbouring leaders, suggesting that some followers may be using this as a strategy to avoid competition with leaders and offset their disadvantage.

Can spacing offset the disadvantage of followers?

Spacing has been shown to have adaptive value (Arak et al. 1990) for calling males. While Cade (1981) showed that aggregation of males attracted more females, Arak et al. (1990) suggested that on a small spatial scale (i.e. within a chorus) it benefits individual males to space themselves apart rather than clump together. This is possibly to avoid competition from other males (Arak 1983). Using a simulation that modelled two sound sources (males), Forrest & Green (1991) argued that quieter males

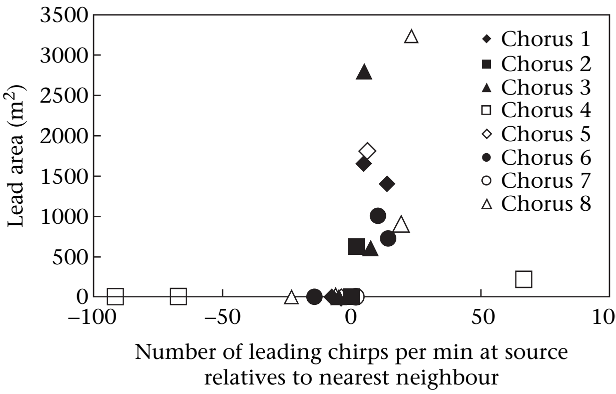

Figure 7. Areas in which the males led their nearest neighbours in relation to the number of leading chirps with respect to their nearest neighbours at source. Each point represents one male. Different symbols represent males from different choruses. One chorus (chorus 5: animal 1: number of leading chirps at source = 282, lead area = 0 m^2; animal 2: number of leading chirps at source = 410, lead area = 0 m^2; animal 3: number of leading chirps at source = 1571, lead area - = 72 401 m^2) has been excluded to enable scaling that allowed clear representation of the other males in the figure.

Table 3. Chirp periods(s) of males across nights

Male identity	16 Aug	18 Aug	20 Aug	22 Aug	24 Aug	25 Aug	26 Aug	27 Aug	29 Aug	30 Aug	31 Aug	1 Sep
KPB				0.574	0.652	0.580		0.539	0.533	0.526	0.609	
VWK	0.644		0.584	0.555	0.593	0.540	0.597					
WBP			0.574		0.584	0.544	0.581			0.566	0.581	0.531
PBW				0.565	0.628	0.581	0.649	0.539				0.544
KPP	0.627	0.546		0.547	0.601		0.572					
VKK		0.534		0.503	0.592		0.549			0.527		
WPK		0.536						0.529		0.530	0.570	
BBW			0.588	0.451	0.645	0.519						
VBP									0.543	0.529		0.522
WKW							0.577			0.463	0.529	0.531
PWV									0.541	0.532	0.537	0.556
PPP	0.634	0.490				0.545						
WBW	0.606		0.584	0.560								
BVP	0.640	0.579	0.576									
VBV	0.656	0.558			0.614							
VBW	0.644						0.578			0.525		
WVB			0.535	0.543	0.637							
VKP			0.539			0.573					0.614	
KKP				0.544	0.599							0.522
BVK					0.571	0.562						0.563
PWK										0.550	0.582	0.563
Mean period (s)	0.636	0.540	0.569	0.538	0.611	0.556	0.586	0.536	0.539	0.527	0.575	0.541
Mean temperature (°C)	22.49 ±0.58	24.86 ±0.62	24.36 ±0.82	24.98 ±0.7	23.54 ±1.14	23.99 ±0.79	23.70 ±0.43	24.63 ±1	24.90 ±0.35	24.43 ±0.44	23.96 ±0.57	25.11 ±0.52

Columns correspond to single nights.

would gain the most advantage by spacing themselves outside the sound field of the louder males. Farris et al. (1997) further showed empirically that quieter sound sources had a greater advantage when further from the louder sound source but that females were less discriminating when the absolute intensities of both were high.

In our study, quieter males in the choruses were spaced such that they were either entirely or partially within the sound field of the loudest male, suggesting that they may gain some advantage by being closer to the loudest male, perhaps because when a female is close to the males, the intensities are so high that she does not discriminate between the two. This is also suggested by studies (Oldfield 1983, 1984) showing that the spike frequency of ascending auditory interneurons of bushcrickets saturates between 30 and 70 dB above their threshold. If *M.* 'Chirper' has similar physiological limits and a hearing threshold of 30 dB SPL, this would mean that the female would not be expected to discriminate between intensities in the range of 70–100 dB SPL, which is the range of intensities she would encounter when close to males. Another interesting effect of spacing was that despite leaders being on average louder at source, the mean loudest area was not significantly different between leaders and followers. This suggests that followers can space themselves such that they are able to compensate for their lower SPLs.

Spacing, however, does not appear to help followers offset their disadvantage in terms of lead. If females are randomly spaced in the field, there are areas in which some followers will lead because of differing sound transmission delays from the males in a chorus to the female. Our simulations show that no followers had areas in which they led their neighbouring 'leaders'. Thus leaders at source are perceived as leaders throughout their acoustic range.

Followers may therefore be able to offset their disadvantage only through calling more often when leading males are silent. Examples of this strategy were seen in this study. The degree of success of this strategy in attracting females cannot, however, be evaluated without a complete knowledge of how females make their choices. Experiments with females using realistic spacing patterns, intensities and timing relationships between calls are necessary to estimate how successful these strategies actually are.

Lead Consistency across Nights

Even if followers were unable to compensate for their disadvantage through other call features, it is possible that they get to lead on other nights. If this were so, we would expect to see no consistent leaders and followers across nights and poor repeatability of leading in calling males. Repeatability of song traits is an important measure as it sets the upper bound for the heritability of the trait (Falconer & McKay 1996). Previous studies on crickets and grasshoppers demonstrated that certain song traits have a moderate or high repeatability. Butlin & Hewitt (1986) found in the grasshopper *Chorthippus brunneus* that chirp length and syllables per chirp had a repeatability value of 0.56 while Hedrick (1988) found in the field cricket *Gryllus integer* that the proportion of calls with long bouts had a repeatability of 0.85. In studies of anurans, call rate was found to have low or moderate repeatability (Sullivan & Hinshaw 1990: 0.47; Sullivan & Hinshaw 1992: 0.2–0.5; Wagner & Sullivan 1995: 0.08–0.33).

Our results from *M.* 'Chirper' in the field show that the chirp period of males has lower repeatability than the song traits of various species in any of these studies. While it is known that chirp period does change with age (Ritchie et al. 1995), the brief period over which our study was conducted argues against age being an explanation for the variation in chirp period across nights. Furthermore, our repeatability analysis used the values of chirp period after regressing them against temperature. Therefore, temperature cannot be an explanation for the fluctuations in individual chirp period.

The low repeatability of the chirp period of males relative to their nearest neighbours and the other males calling on a night shows that even with respect to their immediate competitors males do not remain leaders or followers night after night. This could either be a direct result of the low repeatability of chirp period or because males have different partners on different nights or both. In our study, no male had the same nearest neighbour on 2 different nights. Thus both explanations could account for the poor repeatability of relative chirp period.

The lack of repeatability suggests that chirp period is not a highly heritable trait in this species (Falconer & McKay 1996). As lead probability is dependent on the chirp period (Nityananda & Balakrishnan 2007), low heritability of chirp period implies that males are not genetically leaders or followers. It also implies that females cannot use either lead or chirp period as an indicator of male genetic quality.

As Wagner & Sullivan (1995) argued, call period may instead reflect the phenotypic condition of the male and this might explain the low repeatability, as condition dependence could cause high within-individual variability in the trait. Studies examining the influence of male condition on call parameters have typically used different nutritional regimes to look at phenotypic condition. Some of these studies have found that signalling is condition dependent (Simmons et al. 1992; Wagner & Hoback 1999; Scheuber et al. 2003) and that the choice of mates reflects this condition (Holzer et al. 2003). Hedrick (2005) showed in the field cricket *G. integer* that call bout duration, a heritable trait that influences female choice, is dependent on male condition. However, Gray & Eckhardt (2001) found that the number and period of high-frequency ticks and the interphase interval of the courtship song of *Gryllus texensis* are independent of male condition. In the katydid species *M. elongata* (which is closely related to our study species), Hartbauer et al. (2006) also argued that chirp period is independent of condition. If this proves to be the case in *M.* 'Chirper' as well, then the preference of females for leading males may be the result of a sensory bias (Ryan & Keddy-Hector 1992; Römer et al. 2002). This hypothesis is supported by the observation in *M. elongata* that the follower's signal is suppressed in the nervous system of the female by contralateral inhibition, a strategy for effective sound localization (Römer et al. 2002).

Acknowledgments

We are grateful to the Ministry of Environment and Forests, Government of India for funding this project. We thank Manjari Jain, Natasha Mhatre and Swati Diwakar for help with call recordings made in the field and Sumit Dhole and Ismene Fertschai for help with the chorus recordings and the attenuation measurements. We also thank Amrita Neelakantan, Giby Kuriakose and Smita Nair for help with marking the animals and Heiner Römer and Michael Greenfield for their helpful comments on the work.

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