

# Female reply strategies in a duetting Australian bushcricket, *Caedicia* sp. (Phaneropterinae: Tettigoniidae: Orthoptera)

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## Summary

Duetting is common between the sexes of phaneropterine bushcrickets (Phaneropterinae: Tettigoniidae: Orthoptera). In this paper we describe the complex duet of an undescribed Australian species within the genus *Caedicia*. The male's call consists of three parts, of which the final part contains information of the species' identity and most reliably elicits the female's response. The timing of her reply usually occurs within a period of about 1 s after the male has completed his signal but may also start during the male's call. Females reply with brief clicks ranging from 1 to >10, adjusting this reply number to changes in male call duration and intensity. By using computer-synthesised calls, we discovered that the female

times her reply both from cues within the male call, when she starts the reply before its conclusion, and from the end of the call, in the case where the reply follows the male call. As the number of clicks in the reply increases so the interval between clicks decreases; the female fits her entire reply within a critical time window following the male's call. The male call intensity had a marginal effect on female reply strategy. We suggest a model based on levels of female motivation, by which females may set the number of clicks in reply as well as the reply latency.

Key words: duet, acoustic behaviour, reply strategy, bushcricket, Tettigoniidae, Orthoptera.

## Introduction

The simplest definition of a duet is a dialogue of two voices and, for most animals the duet is marked by signals with a fixed temporal relationship to each other (Greenfield, 2002; Bailey, 2003). Both chorusing among males (Greenfield et al., 1997) and duetting between the sexes (Robinson, 1990) are common features of bushcricket (katydid) communication and duetting is almost universal among one subfamily, the Phaneropterinae (Tettigoniidae: Orthoptera) (Robinson, 1990). In a typical phaneropterine duet, the male calls and the female replies to this call with a series of clicks and, most often, the male then searches for the replying female (Spooner, 1968). Which sex takes on the searching role may change, however, and often, where males do not reach a female, the female may both reply and search for the male call (Spooner, 1968, 1995; Bailey and Field, 2000).

The acoustic signal normally contains three essential pieces of information: the identity of the caller, its location, and the distance between caller and listener. For bushcrickets the species' identity is encoded in the temporal structure of the call (Bailey, 1991), but for many phaneropterines the male's signal is extremely short, consisting of barely more than one or more syllables of less than 1 ms. The female reply is rapid and equally brief, often with latencies less than 25 ms (Robinson et al., 1986; Zimmermann et al., 1989; Robinson, 1990; Dobler et al., 1994). In these cases, where there is minimal information with respect to the amplitude modulation of the signal,

recognition by the searching male is achieved solely by the delay of the female reply, and the specificity of this delay may be constrained by a few milliseconds (Robinson et al., 1986; Heller and Helversen, 1986; Zimmermann et al., 1989). If the female calls outside the species' time window, the male may fail to commence searching and ignore the female (Zimmermann et al., 1989; Helversen et al., 2001).

By comparison, other phaneropterine duets consist of long complex male calls, with the female producing a reply of varying length (Spooner, 1968; Shaw et al., 1990; Bailey and Field, 2000). In these cases the male has the capacity to provide information on both species' identity and female preferred traits, such as size or the ability to provide a nuptial gift. The nuptial gift of bushcrickets is a spermatophore consisting of a substantial protein-rich spermatophylax attached to the sperm ampulla (Gwynne, 1986). If, for this or any other reason, females choose among males using the song, then call duration or complexity has the potential to determine the direction of female preference (Tuckerman et al., 1993). In these cases the number of replies made by the female may be indicative of a preference between males, and in some species the length of reply may provide the male with a guide as to the female's readiness to mate (Galliart and Shaw, 1996).

Here we examine three aspects of duetting in an undescribed species of Australian bushcricket within the phaneropterine genus *Caedicia*. This species has evolved a duet in which

males provide a long and complex call and the female replies to elements in the call with a variable number of clicks. Our first question concerned female reply strategy. If, as in *Scudderia cauvicauda*, call duration is an important cue for female preference (Tuckerman et al., 1993), then duration should be correlated with the number of female replies. In this context, we also examined whether the intensity of the male call influenced the female reply as intensity may indicate a preferred larger or closer male. Finally, in *Caedicia*, as with most phaneropterines, the female reply to the male call falls within a species' specific time window and so we investigated the cues within the male call used by the female to time her reply (Bailey and Hammond, 2003). When females produce multiple clicks, what mechanisms are available to maintain this train of clicks within the critical time window? She may either start her reply at a fixed time relative to the male call allowing the multiple clicks to extend beyond the time window, or she can start her reply early. In this way most of her calls should fall within the critical time window necessary for male recognition. But such a strategy is complex in that the starting point of her reply will be determined both by her motivation and by different cues within the male's call.

### Materials and methods

#### *The insect – Caedicia species 10*

The genus *Caedicia* is a common macropterous phaneropterine occurring across arid Australia, particularly where there is spring flowering *Acacia* and eucalyptus scrub in temporary run-offs or along semi-permanent waterways. The taxonomy of the Australian Phaneropterinae is incomplete, and for this reason, we give the species used in this study a numeric attribution – *Caedicia* sp. 10. We are aware of at least two other species of *Caedicia* with very similar morphology in Western Australia, but with different call patterns. However, although designating this species as *Caedicia* sp. 10 in this paper, for convenience and ease of reading we refer to the species simply as *Caedicia*. Voucher material is housed at the Australian National Insect collection (ANIC) and at the University of Western Australia.

Juveniles and adults were collected from the Gasgoyne and Murchison regions of Western Australia (Kennedy Ranges and Greenough River) during spring (July–November 2000), and housed in a temperature-controlled insectary with a reversed light/temperature cycle (21:00–09:00 h light, 25°C; 09:00–21:00 h dark, 20°C). Juveniles were kept together in large cages, but males and females were acoustically isolated once they had emerged as adults.

#### *Recording, call synthesis and female reply*

Field-captured males were recorded within an anechoic room held at 20±1°C via a Bruel and Kjaer 1/2" 4133 microphone (Naerum, Denmark) connected to a B&K 2209 sound level meter as a pre-amplifier. The signal was digitised on a computer running Signal© 3.1 (Engineering Design, Belmont, USA) with a sampling rate of 250 kHz. Using the

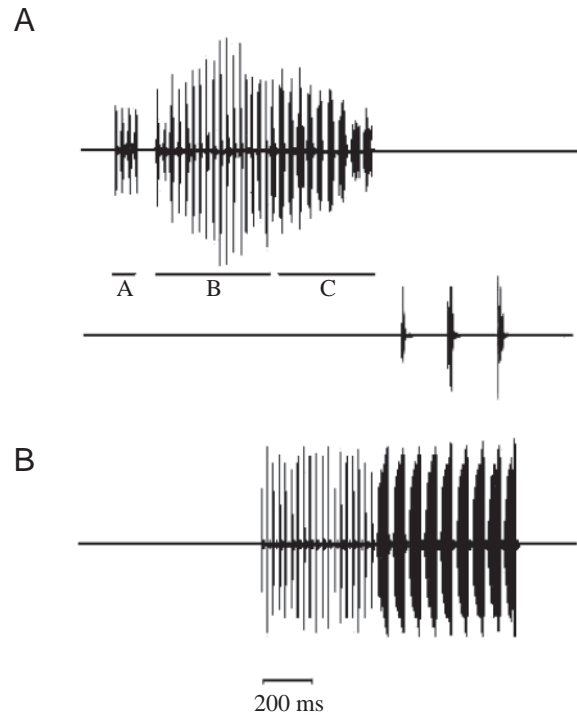


Fig. 1. (A) The male–female duet showing a male natural call (above) with a female three-click reply (below). (B) Synthesised call of 19 'short' syllables forming part B and 9 'long' syllables of part C. All traces share the 200 ms time marker.

editing function of Signal, we excised and saved a single example each of a short and long syllable (see Results for call description). To construct synthetic calls we simply pasted a series of the two sample syllables together to create calls with different combinations of the two syllable types. We made the intensity of each component equal, giving an even sound envelope to the entire call (Fig. 1B). All subsequent call manipulation and delivery was controlled by the Signal software environment.

We established the critical elements of the male call that evoked the female reply, first by removing parts B and C from the call, and then part C leaving parts A and B. To this end all females were tested once in an open arena where we recorded female replies to each randomly assigned modified call. Female *Caedicia* do not respond to part A alone ( $N=13$ ). The inclusion of part C would appear important, as females timed their reply either to elements within this section of the call or to its conclusion. Thus, removing part C but retaining parts A and B increased the variation of reply latency by an order of magnitude (Variance ratio test:  $F_{5,9}=12.13$ ,  $P<0.05$ ). The critical cue for timing had been removed and so, as we were only interested in the timing of the female reply, we combined B and C as the model song.

Reference to the male call follows commonly used terms in that a syllable is one wing movement, and a chirp refers to clearly delineated groups of syllables. We use the term click, rather than syllable, to describe each element of the female

Table 1. Parameters of synthesised calls used in experiments testing temporal variation on female response

| Treatment | Short syllables |                    | Long syllables |                    | Call duration (ms) |
|-----------|-----------------|--------------------|----------------|--------------------|--------------------|
|           | Number          | Range of variation | Number         | Range of variation |                    |
| 1         | 8               | -2 s.d.            | 9              | Mean               | 1856               |
| 2         | 30              | +2 s.d.            | 9              | Mean               | 3154               |
| 3         | 19              | Mean               | 4              | -2 s.d.            | 1736               |
| 4         | 19              | Mean               | 14             | +2 s.d.            | 3274               |
| 5         | 19              | Mean               | 9              | Mean               | 2505               |
| 6         | 19              | Mean               | 19             | +4 s.d.            | 4043               |

The mean, species' call pattern is represented as Treatment 5, with values of short and long syllables varied by up to 4 s.d. from this mean.

reply as this sound is not made by homologous structures to the male tegmina (Robinson, 1990).

Females usually reply within a defined period following the male call and this critical latency of reply is referred to as the reply time window (Zimmermann et al., 1989; Robinson, 1990). The male uses this latency to recognise and locate the responding female. For *Caedicia* the reply time window was measured from the end of part C. As between-female variation in the number of clicks produced in reply to the male call was much greater than the within-female variation (due to treatments within an experiment), it was necessary to determine the level of experimental variation that would otherwise be hidden by between-female variation. To this end we used a non-parametric equivalent of a one-way repeated measures analysis of variance (ANOVA), the Friedman Test (Zar, 1984) to test for the effect of temporal pattern on female response.

#### Experiment 1: Temporal variation

In order to manipulate call duration we created six call types with differing numbers of short and long syllables. Treatments involved changing the lengths of parts B and C from mean values to 2 and 4 standard deviations (s.d.) above and below the mean (Table 1).

Each caged female was introduced to the anechoic room 15 min before the trial. We presented 24 calls to the female with 12 s between each presentation. The speaker was placed 1.5 m from the female, with stimulus intensity of 81 dB SPL (Re. 20  $\mu$ Pa) measured at the position of the female, which was close to natural sound levels at this distance. In order to obviate errors in measuring Sound Pressure Levels (SPL) of very short signals, we calibrated the call against a pure tone of equivalent peak-to-peak level. All recordings and measurements of SPL used a Bruel and Kjaer 4133  $\frac{1}{2}$ " microphone. Calls were played via a Genexxa<sup>®</sup> 12-1971 amplifier through piezoelectric speakers held 15 cm from a carpeted floor. Analysis of natural and broadcast calls showed close frequency matching.

The six treatments were presented four times within a trial, with the order of all 24 calls randomised. If the female was unresponsive after 2 min, the trial was abandoned. All trials were recorded for temporal data analysis on audiotape (Walkman WM-D6C; Sony) using two electret microphones, with one channel recording the stimulus and the other the female response. Tapes were subsequently analysed using

Signal software, which allowed rapid assessment of temporal details of call and reply.

The mean number of clicks produced by each female was consistently variable, ranging from a mean of  $0.54 \pm 0.20$  clicks for the female producing the fewest number of clicks to  $6.6 \pm 0.21$  for the female producing the most clicks ( $N=17$ ). Hence, variation of within-female click number is low while that between-females tends to be high. For this reason changes in female response to each treatment must account for any variations between female. The Friedman test (Zar, 1984), a non-parametric equivalent of repeated-measures ANOVA, was considered valid for these reasons; the distribution of scores within each treatment is clearly not parametric. And so a rank (1-6) was calculated across each individual for each treatment based on the mean number of clicks produced. The test statistic was then calculated from the sum of ranks within each treatment.

#### Experiment 2: Intensity variation

A call with mean values of 19 short syllables and 9 long syllables in parts B and C was synthesised from the standard call (Fig. 1B). Intensity was controlled in a stepwise manner using Signal software. We created three treatments that mimicked a male at half and twice a distance represented by a speaker at 81 dB SPL measured from the female (see above). To achieve this we presented synthesised calls at 75 dB (-6 dB) and 87 dB SPL (+6 dB). As indicated above, call intensity of 81 dB represents a male at approximately 1.5 m from the female. An effective doubling or halving of distance between caller and receiver was achieved by presenting signals at two levels either side of 81 dB. In addition to the usual loss of sound through vegetation (excess attenuation), sound attenuates by spherical spreading from a source by approximately 6 dB per doubling of distance.

As with the first experiment, each caged female was acclimatised to the anechoic room for at least 15 min. We then presented the female with 24 repeated calls at the same intensity separated by 12 s. This series of 24 calls was repeated over a range of three intensities selected in random order with a between-presentation interval of 5 min. As with the experiments on temporal variation, we recorded the response of the female onto cassette tape and subsequently analysed temporal data.

As indicated in the Results, there was a confounding influence of high between-female variation in the number of clicks produced in reply to the male call. To overcome this interaction we standardised scores of the number of clicks for each female before further analysis and so countered any between-female effect. That is, the distribution of scores for each female was transformed (Zar, 1984) to a distribution with a mean of zero and  $S.D.=1$ . Thus, a score of 1 indicates a number of clicks 1  $S.D.$  above the mean for any individual, while a score of  $-1$  would result from a number of clicks 1  $S.D.$  below the mean of that individual. Using this method, scores become comparable among females.

## Results

### *Call description – the duet*

Males commonly call from the outer branches of trees or bushes, and we describe the call as having three sections, parts A, B and C (Fig. 1A). The call is often complex, highly variable and with extreme ranges of intensity throughout. We found that males may extend portions of the call and leave other sections out, and in addition may add extremely short syllables to the end of the call. Such additional sounds are often in response to the presence of other males or, as a response to neighbouring duetting pairs.

Part A of the call is a series of short chirps made up of syllables, where one chirp is shown in Fig. 1A. As indicated above, part A is often absent from the call and females rarely respond to these short chirps, compared to a consistent response to parts B and C. Within these sections of the song, syllables may be classified into two types by duration, ‘short’ and ‘long’. Short syllables (mean  $\pm$   $S.D.=15.54\pm 2.36$  ms,  $N=7$  males, 20 calls from each male) are most common and characterise part B, while long syllables (mean  $\pm$   $S.D.=54.65\pm 6.76$  ms,  $N=7$ , 20 calls from each male) are characteristic of part C. The entire call (B+C) has a mean duration of  $1150.5\pm 156.5$  ms ( $\pm$   $S.D.$ ,  $N=15$ ). The section of the call that we refer to as part B comprises a mean of  $19.16\pm 5.49$  ( $\pm$   $S.D.$ ,  $N=15$ ) short syllables, while part C consists of a mean of  $8.96\pm 2.47$  ( $\pm$   $S.D.$ ,  $N=15$ ) long syllables. The duration of these components also varies with the short syllable section (part B) lasting  $664\pm 173.9$  ms (mean  $\pm$   $S.D.$ ,  $N=15$ ) and the long syllable section (Part C)  $492.5\pm 92.3$  ms (mean  $\pm$   $S.D.$ ,  $N=15$ ). The coefficient of variation (CV) of the length of each section of the call is 23% for short syllables and 19% for long syllables. Call frequency is broadband between 10 and 25 kHz with the main power close to 15 kHz. However, while not considering the role of frequency in this study, we ensured that equipment recording and delivering the calls included this frequency range (see below).

Over 95% of female responses occur during or after part C and consist of one or more brief clicks that may start during part C or from the end of the male call; the reply can last up to 1 s. In both experiments, the number of clicks produced by different females was highly variable, regardless of treatment (Experiment 1, one-way ANOVA:  $F_{6,391}=60.99$ ,  $P<0.0005$ .

Experiment 2, one-way ANOVA:  $F_{6,497}=213.81$ ,  $P<0.0005$ ). That is, different females had tendencies to produce different numbers of clicks in response to the same stimulus. Little information was available to suggest the cause of this variation, although we may speculate on factors such as age, nutritional status and mating history.

### *Experiment 1 – Male call duration and female reply*

Varying call duration by changing the duration of both parts B and C revealed that females preferred call lengths that were close to the species’ mean (treatment 5, Table 1). Female response (measured as rank sum; see Materials and methods) was greatest for mean values of 19 short syllables and 9 long syllables (Fig. 2A,B), and this was significantly greater than any of the other treatments (Friedman test statistic= $16.935$ ,  $a=6$ ,  $b=17$ ,  $P<0.005$ ).

We wished to establish if call duration was related to male size and hence could be used by females to assess calling males. To this end we tested for a relationship between natural call duration and prothoracic length. While Tuckerman et al. (1993) showed a significant correlation between call duration

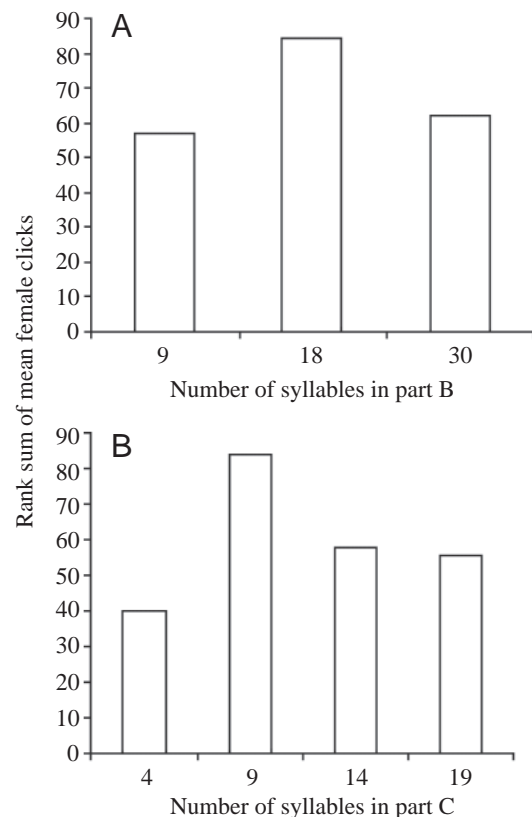


Fig. 2. The response of females to model calls based on varying the number of syllables in parts A and B (see Table 1), expressed as the sum of ranks of mean female clicks (see Materials and methods). (A) Reply of female to part B containing 9, 18 and 30 syllables with part C constant, measured as rank sum of mean female clicks. (B) The same measure to varying syllable number in part C with B held constant.

and the size of the prothorax in *Scudderia curvicauda*, the relationship was weak for *Caedicia* (total number of syllables:  $r^2=0.203$ ,  $F_{1,12}=3.055$ ,  $P=0.106$ ; number of short syllables:  $r^2=0.212$ ,  $F_{1,12}=3.226$ ,  $P=0.098$ ; number of long syllables:  $r^2=0.029$ ,  $F_{1,12}=0.559$ ,  $P=0.559$ ). And, given both a weak relationship between, on the one hand, body size and call duration, and on the other a preference for the mean song structure, it was little surprise to find no relationship between female reply and total male call duration.

#### Experiment 2 – Call intensity and the number of female replies

Three intensity treatments (75 dB, 81 dB and 87 dB SPL) were presented with a between-treatment interval of 5 min. However, the most obvious effect on the number of female replies was not treatment but presentation order. Fig. 3 represents the response of 7 females across presentation order. Because of the high but consistent variation between females, data were analysed by repeated-measures ANOVA. This test showed a significant effect of presentation order on female click number ( $F_{2,12}=12.30$ ,  $P<0.005$ ). The number of clicks produced by each female decreased with each treatment regardless of signal intensity; earlier presentations triggered a higher number of clicks. The confounding effects of order and variation in female response were removed in a two-step process. Data from each female were grouped and standardised. These standardised data were then pooled to extract a cross-female effect of order and each value was then converted to a residual from this order effect. There was a significant and *negative* influence of intensity on standardised click score (one-way ANOVA:  $F_{2,18}=7.24$ ,  $P<0.005$ ). However, the level of variation between treatments in the number of clicks is extremely small (<1 click for each 6 dB change) and so, while this may be an observed effect, we do not know whether such an effect has any biological relevance.

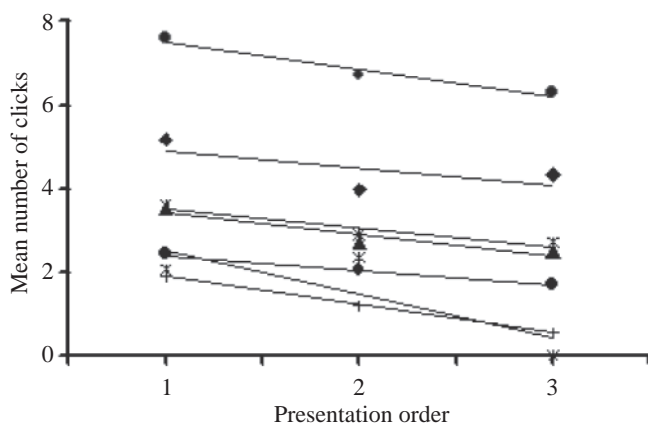


Fig. 3. Effect of presentation order on reply number ( $N=7$ ). Each symbol represents the mean value ( $N=24$ ) from each female with each presentation. While individual females were consistent in the number of their replies, all females reduced the number of replies during the course of the experiment (see text).

#### The female reply window

As indicated above, females replied to the male call with a varying number of clicks. In the experiment in which male call intensity was varied while call duration was held constant, the call's intensity had no effect on the timing of the reply independent of any effects of click number. For this reason, we were justified in pooling all data from all tests. Fig. 1A illustrates a typical female in which the three-click reply is produced some 60 ms after the conclusion of part C of the call.

When females increased the number of clicks they started replying earlier with respect to the start of the synthesised male call. Fig. 4A shows all data for one female, while Fig. 4B shows the mean timing of the first and last clicks ( $N=7$ ). The slope of *changes* in timing, for both upper and lower limits of the call in Fig. 4B, are linear (upper:  $y=1264.12+44.35x$ ,  $F_{1,36}=44.22$ ,  $P<0.0005$ ; lower:  $y=1252.58-57.02x$ ,  $F_{1,36}=143.00$ ,  $P<0.0005$ ).

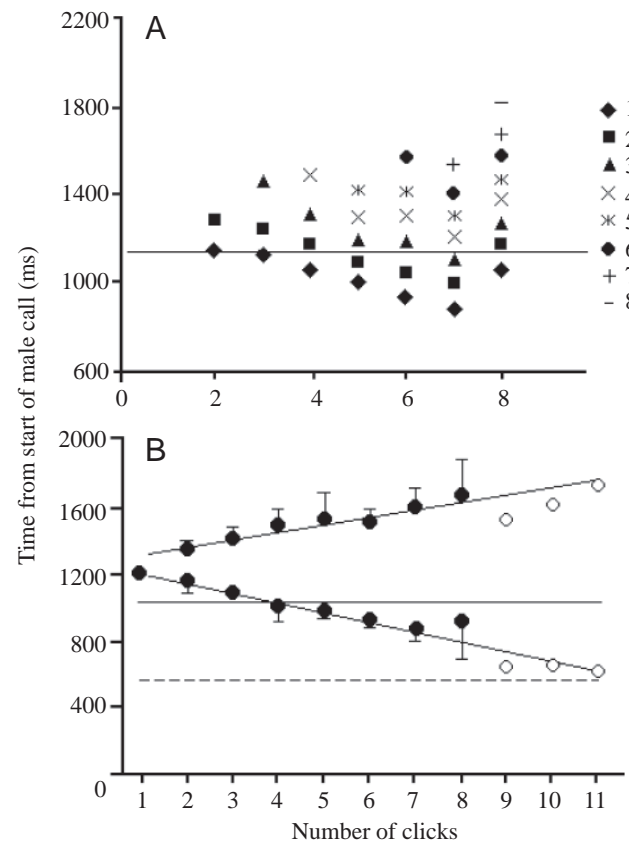


Fig. 4. (A) Timing of one female's reply (animal no. 50) from the start of the male call (zero). As the female increases the number of clicks the entire reply remains within a distinct window between 800–1800 ms. The symbols and associated legend indicate the timing of the first (diamond) to eighth click (horizontal mark) of each set of clicks while the horizontal line indicates the end of part C of the male call. (B) Timing of the first and last clicks of seven females from the start of the male call; the open circles without error bars represent data from one female only. The end of part C of the male call is shown as a solid horizontal line while the end of part B is a broken line. Values are means  $\pm$  s.d.

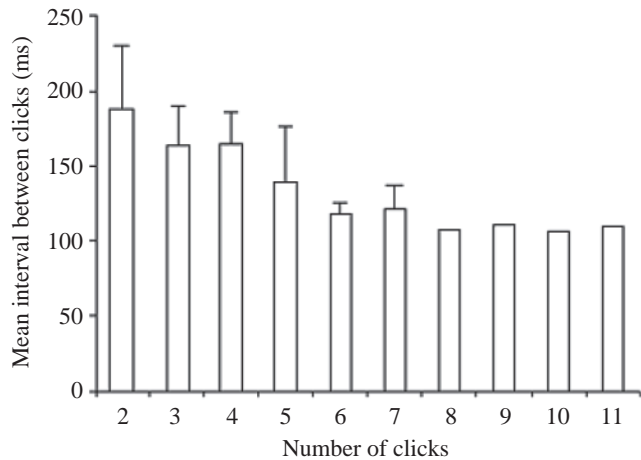


Fig. 5. Mean interval ( $\pm$  S.D.,  $N=7$ ) between successive clicks decreases as the number of replies increases from 2 to 11. Replies 8–11 are from one female.

We wished to know if the slopes, both positive and negative were similar. To this end values of the upper limit were negative-transformed, thus allowing analysis of covariance to test for slope homogeneity. This test showed that the slope of the negative-transformed data (mirror image of last clicks) did not differ significantly from the slope of that taken from the first clicks ( $F_{1,73}=0.78$ ,  $P=0.382$ ). That is, the lines defining the upper and lower limits are mirror images, and so indicate the position and duration of the response window.

The duration of the reply window had an approximate maximum of 1 s with its mid-point close to 220–230 ms after the end of the male call. Moreover, as multiple replies starting within the male call were common, the reply window clearly invaded the male signal and in these cases the timing of the first click could not be from the end of the call.

If we assume that, as in other phaneropterines, the time window is critical for the male reply (*vide* Zimmermann et al., 1989) and hence for the maintenance of the duet, we asked whether females adjust their reply to keep all reply-clicks within the critical time window. Fig. 5 shows that as the number of female replies increased so the interval between each click decreased (one-way ANOVA:  $F_{6,25}=4.10$ ,  $P<0.01$ ).

#### Timing of female reply

We established that the vast majority of female replies are to the male's long syllables – that is, long syllables are the critical stimulus for female response (see supporting data in Materials and methods). In order for the female to maintain her replies within an appropriate reply window there must be a process by which she times her reply from specific acoustic features within the male song. To establish that females in fact use cues in this section of the song we

used data from experiment 1, which examined the effect of variation in the temporal aspects of the male call on female behaviour. We found that females changed reply latency with the changing duration of part C.

Fig. 6A–D shows the shifting or cascading relationship between the timing of the first click of the reply of each series, and to the duration of part C of the signal. While each data set (graph) represents a given number of clicks produced by the female, the data suggest that the female may use more than one cue to determine the timing of the reply. Thus, when part C was short, the reply occurred within a relatively confined window following the end of the male call. However, as the length of part C increased the female began its reply while the male was still calling. There appeared to be a constant delay from the start of part C.

Such timing tactics appeared to be also dependent on the number of clicks produced by the female. The more clicks in a female's reply the more likely she is to time her reply from the start of part C rather than from the end of the male's song. And so in order to keep her click series within the reply window, the female must choose to time her response from a cue *within* the song (presumably the start of the second syllable in part C) or from the *end* of the song. Clearly, if the change from short to long syllables is the critical cue then there is no

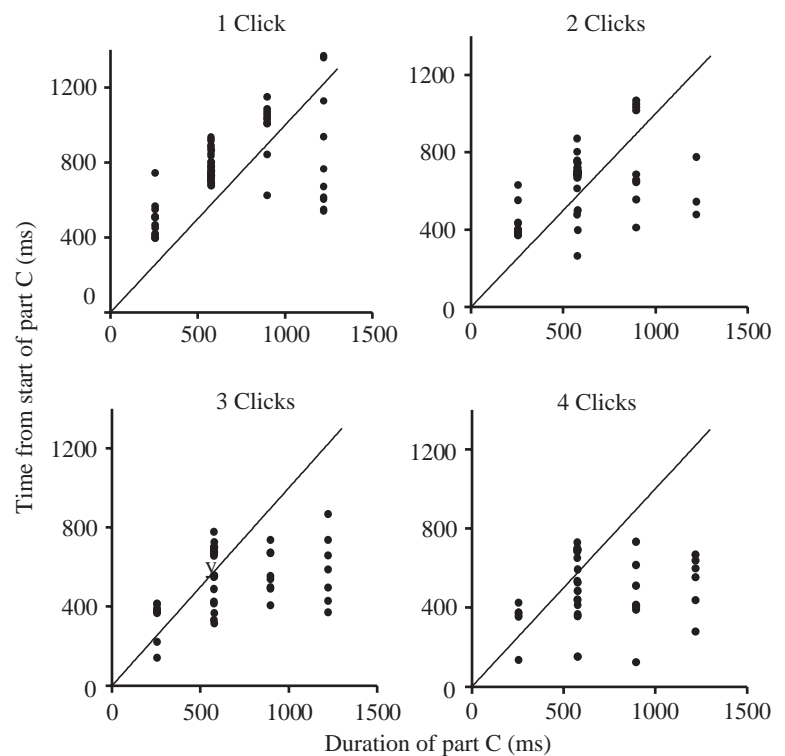


Fig. 6. (A–D) Timing of the first click of the female reply with changing duration of part C. y-axis values are from the start of part C while the diagonal line represents the timing of the end of the song. As females increase the number of clicks (from 1 to 4 clicks) and the duration of part C increases the first click is more inclined to fall within the male call – compare upper left to lower right in each panel.

information until the end of the first syllable and the start of the second in part C.

## Discussion

### *Call type and female preference*

Discussions of reply strategies within the duetting Orthoptera have focused on species' identity and mate location (Hartley and Robinson, 1976; Helversen et al., 2001). Recent studies, have however suggested that variation in female reply within a duet could reflect female call preference (Tuckerman et al., 1993; Galliard and Shaw, 1996) or even searching strategy (Spooner, 1995; Helversen et al., 2001). When estimating female call preference the experimental design can take advantage of the simplicity of the duetting system; the female varying her reply based on traits in the male call. Reply rate and reply number (clicks) then have the potential to be indicators of call preference. For example, *Scudderia curvicauda* males call with a long series of syllables for about 1 s with the female responding with multiple clicks some 700–900 ms later (Spooner, 1968). The number of female replies appears correlated with male body mass in *S. curvicauda*, which is a trait likely to influence female fitness (Tuckerman et al., 1993).

While female *Caedicia* adjust their reply to variation in male call duration, we could find no reliable association between reply length and possible fitness indicators such as body size or mass. Rather, females were more influenced by the species' character of the call than absolute length; they produced more replies to the population means of both parts B and C. Females rarely responded to part A alone, and so we presumed that this introductory section of the call serves to either advertise the call's main element to the female, or perhaps has a role in male–male competition.

### *Female reply window*

Several studies have demonstrated the presence of a temporal reply window following the male call (Robinson et al., 1986; Zimmermann et al., 1989). In many phaneropterines, the female reply is a series of one or more brief clicks, which is a format that allows little scope for conveyance of species' identity. However, because females respond during a defined window, the male can interpret the low-information clicks as those from a conspecific. We found that female *Caedicia* confine their replies to the centre of the window wherever possible. A single click falls on average some 200 ms after the male call and replies with greater numbers of clicks are clustered around this central point (Hammond and Bailey, 2003). We suggest that this maximises the female's chance of having the clicks appear in an individual male's critical time window; he will notice each click and therefore locate the female. Further, as a female increases the number of clicks in a reply, she decreases the time between each click, so optimising the male's attention.

An interesting consequence of this behaviour is the tendency for the female to begin replying before the male has stopped

calling. It is as yet unknown whether a male will recognise female clicks that overlap with his own call, but Shaw et al. (1990) describe the response of female *Amblycorypha parvipennis* as occurring during the song. They found that 96% of female responses occurred during the pause between syllables; females of this species time their responses to this brief period of silence. In contrast, when *Caedicia* females respond during the male's song, they do not exploit a period of silence. However, if hearing in bushcrickets is similar to crickets (Grylloidea) then males may well be able to hear a female call while calling. Poulet and Hedwig (2002) have recently demonstrated a central nervous system corollary discharge that reduces the neural response to self-generated sounds and so protects the cricket's auditory system from self-induced desensitisation. Further investigation into the phonotactic response of the male to the female may answer this question and reveal whether replying during the male song is in fact a useful strategy, or is merely a by-product of producing greater than average number of clicks.

### *Male song cues for female reply*

We show that female *Caedicia* can use a range of cues within the male song for timing her reply and these may be the end of the song and/or elements within the part C. From our experiments it would appear that females require at least 200 ms of part C of the song to reply. As indicated above, the start of the first syllable in part C is indistinguishable from the repeated syllable of part B, and only after the completed first syllable of part C is there sufficient information for timing the reply. In most phaneropterines the reply begins only at the end of a call, and sometimes after the male has produced a distinct trigger pulse (Heller, 1990; Bailey and Field, 2000; Stumpner and Meyer, 2001). Interestingly, in the short-calling *Poecilimon ornatus* (<50 ms), Heller et al. (1997) found that increasing the number of syllables in the male call, which effectively increased call duration, resulted in the female timing her reply from the start, rather than the end of the male call. However, although instructive in this context, the authors used extreme values of male call duration that were unlikely to occur in nature. Despite this reservation, the observation appears consistent with *Caedicia* in that female reply is dependent on at least two decisions: how many clicks will form the reply and whether to use the start or the end of part C as a cue. Clearly, these decisions are related in that the rate of click production will be dependent on the timing of the reply; earlier timed calls of longer duration will have a shorter interval between clicks. We suggest that the length of reply, and thus whether the start (first 200 ms) or the end of part C is used as a cue, may be dependent on female motivation. Also it is possible that the propensity to call may combine with information from the male call, and so determine the number of clicks she produces.

Greenfield et al. (1997) model the call interaction of alternating and synchronising acoustic insects as a shifting threshold of an oscillator. In that model the oscillator has a fixed periodicity, or phase–response curve, and once set

completes its cycle until it is reset. In their model the acoustically responding insect of an alternating pair of males is affected by the timing of one of the partner's call; the oscillator is reset once one male hears the next alternating or synchronising call of its neighbour. Such a model is perhaps useful in explaining the events we describe in this paper.

We suggest that the duet of *Caedicia* is maintained by the recognition of one or two long syllables at the start of part C and that female reply tactics will depend on changing levels of motivational threshold. Thus, if a low-motivated female fails to reach a sufficient threshold to trigger a reply, indicated as a rising function in Fig. 7, she may then start the timing of her reply from the conclusion of the call; her reply will then be timed from the end of the last syllable. However, in the case of a motivated female, a sufficient threshold level may be achieved within part C and, as a consequence, the female will start her reply within the male call.

While a set and re-set model might be one explanation, and in many ways similar to that for alternating insects described by Greenfield et al. (1997), the simpler model is one that involves a continuous change of state between low and high motivation. Indeed, Fig. 4B suggests a smooth transition between 2-click and 8-click replies; there is no stepped function that would support a re-set model. But as with the re-set model, a female that has low motivation (Fig. 7, upper trace X–Z) may require the completion of part C of the call before replying, and for such a female, hearing part C of the call may

only suppress the reply. And so for low-motivated females, in order to optimise the critical time window of the male, and thereby induce male phonotaxis, the female's brief reply is timed from the end of the call. We show how suppression by part C continues until some 100 ms after the conclusion of the male call; females must wait until there is no further call. But the situation may be different for highly motivate females (Fig. 7, upper trace X–Y), where the female recognises elements in part C; the threshold for reply now occurs during this section of the call. Again in order to optimise the male's time window she not only produces more clicks but also at a faster rate; the interval between clicks decreases and she effectively forces her reply within the window. Such a call should not only indicate a female's willingness to mate but would also provide clearer information on which the male might orient.

#### Call intensity

The experiment in which call intensity was varied mimicked the duetting pair calling at different distances. The observation suggested that females respond with fewer clicks to a louder signal and in this way might have a role in distance perception between pairs. However, variation in female click number in response to differing levels of intensity was extremely small (<1 click for 12 dB difference; Fig. 3B) and masked by presentation order; there must be reasonable doubt that such a difference will have biological relevance. If such a difference is indeed relevant to the male, the explanation for this effect may be that closer males require less information for female location and also, there are fewer cues available to an intruding satellite male.

Significantly, presentation order had the most profound effect; the number of female clicks decreased (Fig. 4A) so masking the effects of intensity. Retaining and responding to preceding calls within the duet system is perhaps more common than has been observed within a wider range of insects. Although not explicit, call memory of this nature was first indicated by Busnel et al. (1956), where ephippigerine females continued to track the intermittent call of the male, readjusting its track only when the male's next bout of calling was heard. In complex habitats and with intermittent male call patterns, retaining information with respect to individual recognition and location becomes an essential component of mate searching. Without this, females, or male phaneropterines, would be resetting their search paths to every new sound.

Interestingly, recalling a past sensory event has been demonstrated in duetting fireflies. Souček and Carlson (1987) model the flash duetting of *Photuris versicolor* where females initially flash to their conspecifics until mated and then act as *femmes fatales*, mimicking the flashes of other species. These authors found that response latency of the female was a function of stimulus interval, and the

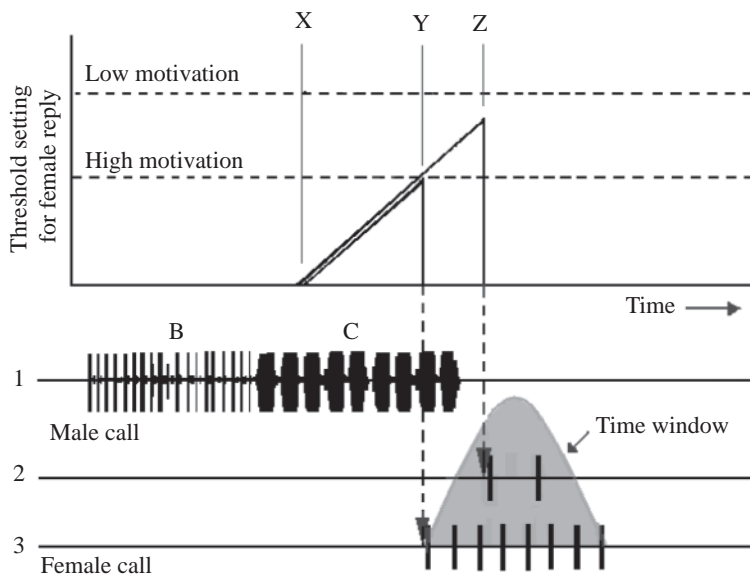


Fig. 7. Long and short reply strategies of female *Caedicia* (traces 2 and 3) to a male call (trace 1) consisting of two parts B and C. Females producing a reply of six clicks have a low threshold at Y (high motivation), rising after recognising elements of part C of the male call (at X). These females call at the start of the species' specific reply window (shaded). Females with high threshold (low motivation) fail to call at the conclusion of part C and, following a brief silent interval, produce 1 or 2 clicks (at Z), which are timed from the conclusion of the call. Note that the click rate of trace 3 is faster than the rate for trace 2.



stimulus–response relationship created what they called a ‘dialogue’. Such dialogues took place during courtship involving conspecifics, while deceptive mimicry or predatory patrolling occurred between heterospecifics. Important in this context was not only a change in response function, from conspecific to heterospecific, but also retention of information from preceding flashes.

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