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A DIVERSITY OF SONGS AMONG MORPHOLOGICALLY INDISTINGUISHABLE KATYDIDS OF THE GENUS *MECOPODA* (ORTHOPTERA: TETTIGONIIDAE) FROM SOUTHERN INDIA

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ABSTRACT

Five distinct song types of the genus *Mecopoda* were found in Southern India. Four were morphologically indistinguishable. Some of them were both sympatric and had synchronous breeding seasons. The songs of these five song types ranged from simple short chirps to highly complex songs with multiple components. The temporal patterns of the songs of the five song types were very distinctive, whereas their spectral features were similar. Component elements of the different songs were distinct despite overall similarity. The song types possibly represent sibling species.

Keywords: Mecopoda*, katydid, cryptic species, morphometry, song types, India*

INTRODUCTION

Katydids and crickets are among the most conspicuous acoustically signalling animals. They produce their calling songs by rubbing their forewings together. This causes the hardened plectrum on the posterior margin of one wing to strike against the teeth of a stridulatory file on the other wing, thus producing sound (Dumortier 1963; Sales & Pye 1974; Ewing 1989). Other parts of the forewing such as the harp and the mirror act as resonators to amplify the song and change its frequency spectrum (Bennet-Clark 1999). Typically, the calling song is produced only by adult males and attracts potential mates from long distances (Alexander 1967). At least amongst sympatric species that call at the same time, each species has a unique calling song with a characteristic temporal pattern and frequency spectrum (Otte 1992 and references therein).

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Katydids belong to the superfamily Tettigonioidea of the suborder of Orthoptera called Ensifera (Otte *et al*. 2005). The katydid subfamily Mecopodinae was first named by Karsch (1886). It consists of six tribes and 25 genera that have not been assigned to any tribe (Otte *et al*. 2005). The tribe Mecopodini belongs to this subfamily and consists of five genera: *Anaedopoda, Characta, Eumecopoda, Macrolyristes* and *Mecopoda*.

There are six reported species of the genus *Mecopoda,* all from Asia (Otte *et al*. 2005). Four of these species have been reported from Indonesia (*M. dilatata*, *M. divergens, M. elongata* and *M. macassariensis*), one from Japan (*M. niponensis*) and one from Sri Lanka (*M. platyphoea*). The only species reported from India is *Mecopoda elongata* (Linnaeus 1758). Previous reports of this species from the Indian subcontinent (Ingrisch 1990; Ingrisch & Shishodia 2000; Ingrisch & Garai 2001) do not have any details of the calling songs. Different song types of this genus have, however, been previously reported from Malaysia (Sismondo 1990; Römer *et al*. 2002), one of them under the species name *elongata*. The name *elongata* has also been given to other song types found in Malaysia (Hoppe *et al*. 2005).

We have found five song types of the genus *Mecopoda* in the state of Karnataka in South India. The individuals of these song types are remarkably similar to each other morphologically and also to images of the species *M. elongata* (Otte *et al*. 2005). Their calling songs, however, differ from the songs of all the Malaysian song types classified as *Mecopoda elongata* (Sismondo 1990; Römer *et al*. 2002; Hoppe *et al*. 2005). The lack of quantitative data on song and morphology in the early records made it difficult to evaluate whether any of the Indian song types that we found corresponded to the originally described species or to assess whether all the song types found should be classified under the species name *elongata*. We have therefore performed a detailed and comparative characterisation of the song and morphology of the five song types with an aim to assess the differences in calling songs and morphology between the five song types.

Another reason for the detailed characterisation is the range of complexity of the temporal patterns of the calling songs found in the five song types. The songs ranged from simple chirps and doublets to two-part calls and complex trills. We investigated the idea suggested by Otte (1992) that complex songs evolve by the combination, addition and removal of component units such as the pulses or chirps of structurally simpler songs.

The five song types have been given the informal names *Chirper, Double Chirper, Two Part Caller, Helicopter* and *Train* based on the perceptual quality of the songs.

METHODS

Song recording and analysis

Calling males were tracked and located by ear in the field. Their songs were recorded in the field using a Sony WM-D6C Professional Walkman cassette recorder and a Sony ECM-MS957 microphone (flat frequency response from 50 Hz to 18 kHz). After each recording, the ambient temperature was measured using a Kestrel 3000 Pocket Weather Station. The animals were captured and later used for morphological analysis.

The song recordings were digitised using a Creative Sound Blaster A/D Card at a sampling rate of 44.1 kHz and downsampled at a rate of 16 kHz for temporal pattern analysis. A customised MATLAB program (Chandra Shekhar, ECE, IISc) was used for analysis of temporal patterns at the level of chirps.

For analysis of the fine temporal (syllable) structure and spectra, recordings were made in the laboratory in a sound proof recording chamber using either a Bruel and Kjaer Sound Level Meter type 2231 with a ¼″ microphone (4939: flat frequency response from 4 Hz to 70 kHz) or a Pettersson Elektronik D 989 Ultrasound Detector (custom made microphone with a flat frequency response from 2 kHz to 200 kHz). These recordings were digitised using a NI-DAQ AT-MIO-16E-2 A/D card at a sampling rate of 200 kHz. After each recording, the ambient temperature close to the calling individual was measured using a Testo 110 thermometer. Spectra were analysed using Spectra Plus (1994, Version 3, Pioneer Hill Software, Washington, USA).

Recordings were obtained from all five song types: *Chirper* (n = 9 males), *Double Chirper* (n = 9 males), *Two Part Caller* (n = 5 males), *Train* (n = 10 males) and *Helicopter* (n = 8 males).

Morphology

Ten males of each of the five song types were collected from localities in and around Bangalore, Gerusoppa, Karkala, Shimoga and Sirsi in Southwest India (Figure 1). These males were tracked by ear in the field and their songs were recorded before collection. The specimens were either mounted dry or preserved in 70% alcohol for morphological studies.

75 quantitative and 61 qualitative characters were measured for each of the 50 animals (10 individuals of each of the 5 song types) using a binocular stereo zoom microscope (Labomed) with a graduated eyepiece or a Vernier calliper (Mituyo). The list of characters is given in Appendix 1.

Statistical Analysis

Song features

The means and standard errors were calculated for different features of each song type. Different features of a particular song type were compared using paired *t*-tests at a significance level of $\alpha = 0.05$. Features adjudged similar across different song types (e.g.: chirps, doublets of chirps) were compared using a one-way ANOVA. If significant differences were seen, these features were then compared pairwise using unpaired *t*-tests at a significance level of $\alpha = 0.05$. Each song feature was regressed against temperature to check for any significant effect of temperature. If a feature of a song type showed a significant change with temperature, it was regressed to the mean temperature at which the songs of the other song types were recorded for comparisons between song types.

Morphological characters

Multivariate analyses of quantitative and qualitative characters were performed separately. For the quantitative characters, the values of all characters were standardized by subtracting the mean value and dividing by the standard deviation of each character (Manly 1986). The standardized values were then used to generate a Euclidean distance matrix that was used for further analysis. For the qualitative characters, each state was given an integer code. These values were not standardised as the integers given were only codes and the values of the integers were unimportant. The codes were used to generate a dissimilarity matrix that was used in further analysis.

The distance and dissimilarity matrices generated as mentioned above were used to perform a cluster analysis (UPGMA: Sneath & Sokal 1973). All statistical analyses were performed using the software package STATISTICA (1999, Statsoft Inc., USA).

RESULTS

Distribution and seasonality

The known distribution of the five song types that we found in the state of Karnataka in South India is given in Figure 1. The song type *Chirper* was found in Bangalore (on the campus of the Indian Institute of Science) and in Shimoga during the monsoon season (August–December). The song type *Double Chirper* was found in deciduous forests and plantations around Karkala in the dry season (December–March). The song type *Two Part Caller* was found in the evergreen

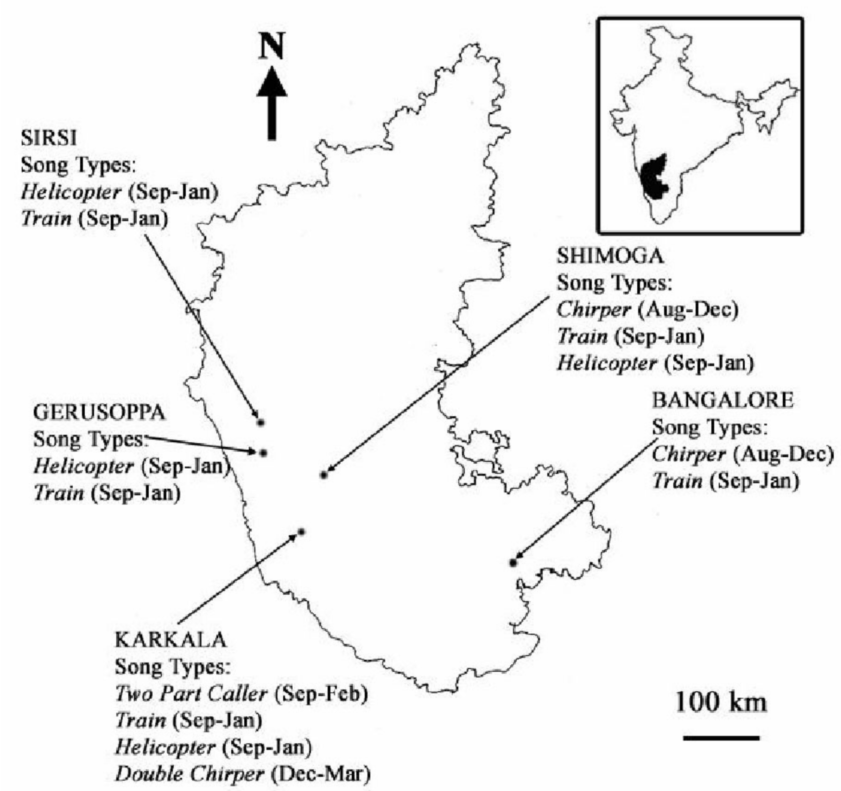


Figure 1. Schematic illustration of the locations of collection sites of the five *Mecopoda* song types in the state of Karnataka, India. Inset shows the location of the state in India.

forests and plantations around Karkala in both the monsoon and the dry season (September–February). The song type *Train* was found in forests and plantations around Bangalore, Gerusoppa, Shimoga, Sirsi and Karkala in both the monsoon and the dry season (September-January). It was also recorded further north in Mahabaleshwar in the state of Maharashtra. The song type *Helicopter* was found in Gerusoppa, Shimoga, Sirsi and Karkala in both the monsoon and the dry season (September–January). It was also found in deciduous forests and plantations around Karkala.

The song types *Chirper* and *Train* were found to be sympatric and synchronous with respect to adult breeding season in some regions (Figure 1). The song types *Train, Helicopter* and *Two Part Caller* were found to be both sympatric and synchronous in most areas where they were found. The song types *Double Chirper* and *Helicopter* were sympatric and synchronous in the deciduous forests and plantations around Karkala. All the song types were univoltine with one breeding season per year.

Song Analysis

Characterisation of the songs of the five song types

The spectra of the five song types were similar, being very broadband with a range of 2–70 kHz (Figure 2). There were, however, minor differences between the spectra of the five song types, especially at the lower frequencies.

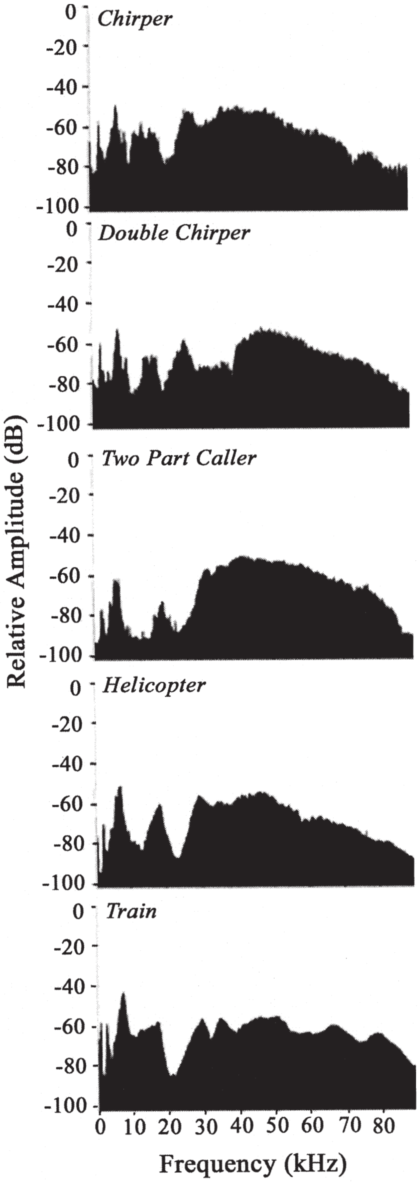


Figure 2. Representative power spectra of the five song types.

The temporal patterns of the five song types were very diverse and ranged from simple chirps to complex trills.

1. Song Type *Chirper*

The calling song consisted of stereotyped chirps with a regular period (483.3 ± 43.5 ms) and duration (109.2 ± 16.8 ms) (Figure 3a, Table 1a). Each chirp was comprised of 7–17 syllables (mean = 10.1 ± 3; Table 2a) that varied in period (mean = 10.4 ± 1.1 ms) (Table 2a). After the first two or three syllables, the syllables alternated between two syllable types (Figure 3b). One of them was higher in amplitude and increased in amplitude over its duration. The other was lower in amplitude and decreased in amplitude over its duration. Successive syllables of both types were greater in amplitude and duration than previous syllables of the same type.

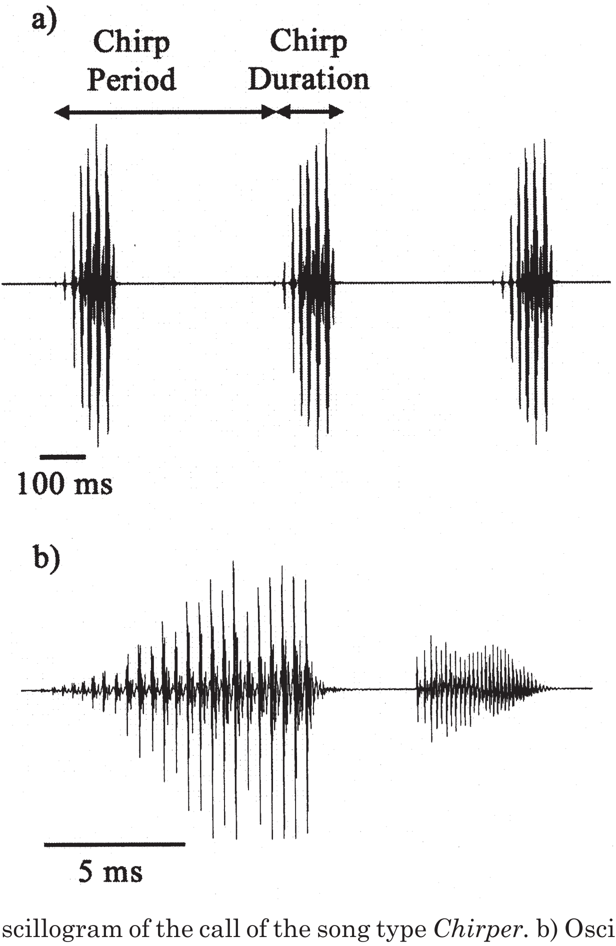


Figure 3. a) Oscillogram of the call of the song type *Chirper*. b) Oscillogram of the two types of syllables present in all the song types.

TABLE 1

Values of chirp level song features of the five song types

Song feature	Mean (± S.E.)	Number of animals	Mean number of units per animal	Mean temperature of recording (± S.D.)
a) *Chirper*				25.6 (0.5)
Chirp Duration (ms)	109.2 (16.8)	10	20.7	
Chirp Period (ms)	483.3 (43.5)	10	20.7	
b) *Double Chirper*				26.9 (0.8)
Doublet Duration (ms)	176.4 (18.7)	10	26.5	
First Chirp Duration (ms)	55.5 (11.6)	10	26.5	
Second Chirp Duration (ms)	54.6 (10.1)	10	26.5	
Doublet Period (ms)	379.3 (18.7)	10	26.5	
Intra-Doublet Period (ms)	121.8 (10.7)	10	26.5	
Singleton Duration (ms)	64.0 (14.3)	7	13.8	
Singleton Period (ms)	266.6 (9.8)	7	13.8	
c) *Two Part Caller**				24.6 (1.9)
Verse Duration (s)	1.8 (0.2)	10	10	
Trill Duration (s)	1.3 (0.2)	10	10	
First Chirp Duration (ms)	87.5 (10.8)	10	10	
Second Chirp Duration (ms)	83.1 (12.2)	10	10	
Verse Period (s)	1.9 (0.2)	10	10	
c1-c2 Period (ms)	293.9 (64.7)	10	10	
c2-t Period (ms)	229.0 (24.5)	10	10	
d) *Helicopter*				23.3 (0.4)
Verse Duration (s)	36.2 (4.4)	10	1	
Duration of Start segment (s)	4.6 (0.9)	10	1	
Duration of Start segment chirps (ms)	87.2 (8.5)	10	13.9	
Period of Start segment chirps (ms)	359.6 (58.2)	10	13.9	
Duration of Trill segment (s)	17.1 (2.9)	10	1	
Duration of chirps in Trill segment (ms)	222.6 (30.5)	10	60.4	
Period of chirps in Trill segment (ms)	260.1 (26.1)	10	60.4	
Duration of End segment (s)	14.4 (4.1)	10	1	
e) *Train*				25 (2.1)
Start segment duration (s)	21.0** (5.0)	16	1	
Duration of repeated sections (s)	1.0 (0.1)	16	12.7	
Duration of chirps in the repeated sections (ms)	28.8 (8.2)	16	175.5	
Duration of bursts in the repeated sections (ms)	394.4 (60.5)	16	12.7	
Period of repeated sections (s)	1.1** (0.1)	16	12.7	
Burst-Next Section Period (ms)	442.1 (66.8)	16	12.7	
Duration of middle segment (s)	5.8 (3.1)	16	1	
Trill duration (s)	68.3 (4.5)	3	1	
Duration of chirps in the trill (ms)	103.4 (28.9)	15	151.2	
Period of chirps in the trill (ms)	118.5 (32.6)	15	151.2	

* Bouts of song where the trill was followed by two chirps was used for analysis.

** Values regressed to 23.3° C

2. Song Type *Double Chirper*

The call consisted of doublets of chirps and single chirps (singletons) (Figure 4). Individual males were observed to produce bouts of both doublets and singletons. Both chirps of the doublets and the singletons were comprised of approximately six syllables (Table 2b) structured similar to those of *Chirper* described above but with a mean period of approximately 11 ms (Table 2b). The values of the different song features are given in Table 1b and Table 2b.

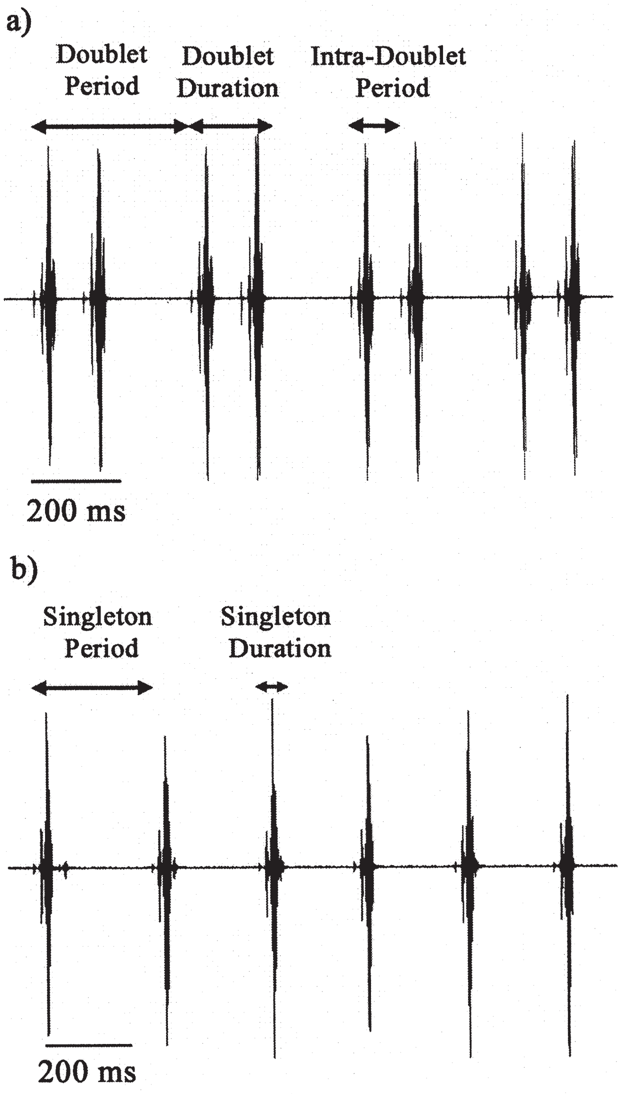


Figure 4. Oscillograms of the call of the song type *Double Chirper*: bouts of a) doublets b) singletons.

The mean durations of the chirps constituting the doublets (first chirp: 55.5 ± 11.6 ms; second chirp: 54.6 ± 10.1 ms) and the singletons (64 ± 14.3 ms) did not differ significantly (Figure 5a, P = 0.45, 0.08 respectively), while the mean intra-doublet period (the time from the onset of the first chirp in a doublet to the onset of the second chirp), was significantly lower than the mean singleton period (Figure 5b, $P <$ 0.001). Interestingly, the mean singleton period of the *Double Chirper* was significantly less than its doublet period (Figure 5b, $P <$ 0.0001, Table 1b).

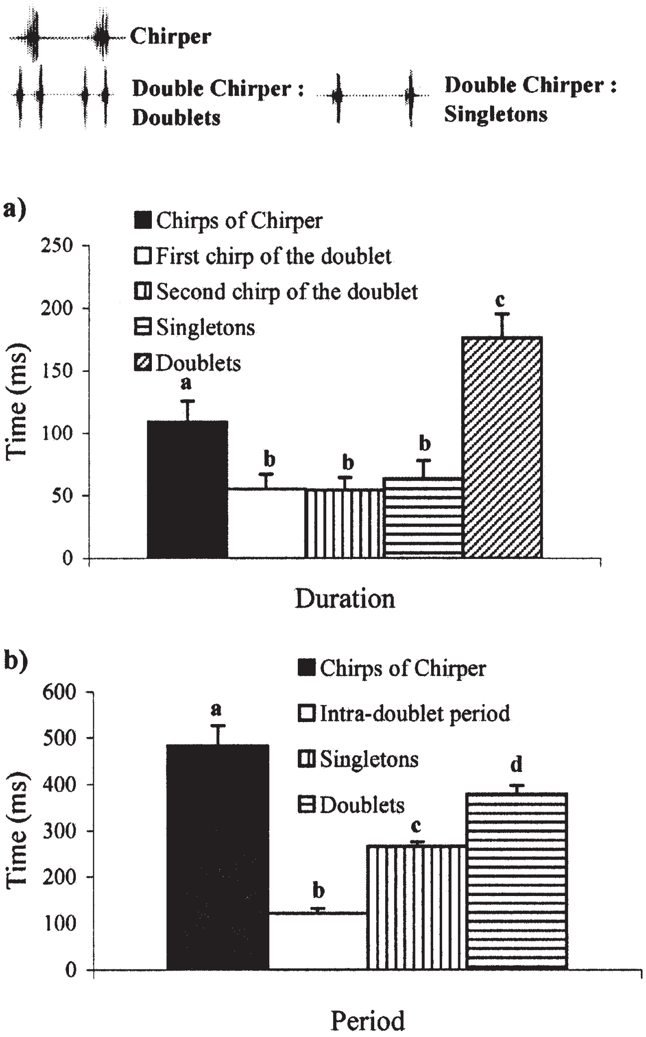


Figure 5. Comparison of mean a) durations and b) periods of the chirps of *Chirper* and *Double Chirper*. Different letters indicate significantly different values (a = 0.05).

TABLE 2

Values of song syllable features of the five song types

Song feature	Mean (S.E.)	Number of animals
a) *Chirper*		
Number of syllables in chirp	10.1 (3)	9
Syllable Period (ms)	10.4 (1.1)	9
b) *Double Chirper**		
Number of syllables in the first chirp	5.6 (0.3)	7
Number of syllables in the second chirp	5.7 (0.3)	7
Number of syllables in the singleton	5.5 (0.5)	7
First Chirp Syllable Period (ms)	10.5 (1)	7
Second Chirp Syllable Period (ms)	10.6 (1)	7
Singleton Syllable Period (ms)	10.8 (1.4)	7
c) *Two Part Caller*		
Number of syllables in the first chirp	7.9 (1.4)	4
Number of syllables in the second chirp	7.6 (1)	4
First Chirp Syllable Period (ms)	9.3 (0.7)	4
Second Chirp Syllable Period (ms)	8.7 (0.4)	4
d) *Helicopter*		
Number of syllables in Start segment chirps	12.4 (1.6)	7
Syllable Period of Start segment chirps (ms)	9 (0.6)	7
Syllable Period of End segment (ms)	10.3 (0.7)	7
e) *Train*		
Number of syllables in the Start segment chirps	2 (0)	7
Syllable Period of Start segment chirps (ms)	19.8 (4.1)	7
Number of syllables in the Trill segment chirps	8.5 (1.1)	7
Syllable Period of Trill segment chirps (ms)	10.3 (2.7)	7

No. of units analysed per animal = 10.
Mean temperature of recording as in Table 1 except for Double Chirper.
*Mean temperature of recording (S.D.) = 29.75 (1.3)

3. Song Type *Two Part*

The call consisted of stereotyped repeated verses. Each verse consisted of a trill followed by two or three short chirps (Figure 6). The verse period was close to two seconds, with the duration of the trill component of the verse being much larger than the duration of the chirps (Table 1c). The mean durations of the two chirps following the trill did not differ significantly from each other (first chirp: 87.5 ± 10.8 ms; second chirp: 83.1 ± 12.2 ms, $P = 0.19$). Each of the chirps was comprised of approximately eight syllables structured similar to those of *Chirper* with a mean period of about 9 ms (Table 2c).

4. Song Type *Helicopter*

The call consisted of repeated verses each consisting of three segments (Figure 7a). The first segment (“Start”) had chirps of short durations and long periods (Figure 7b, Table 1d). Each chirp consisted of about

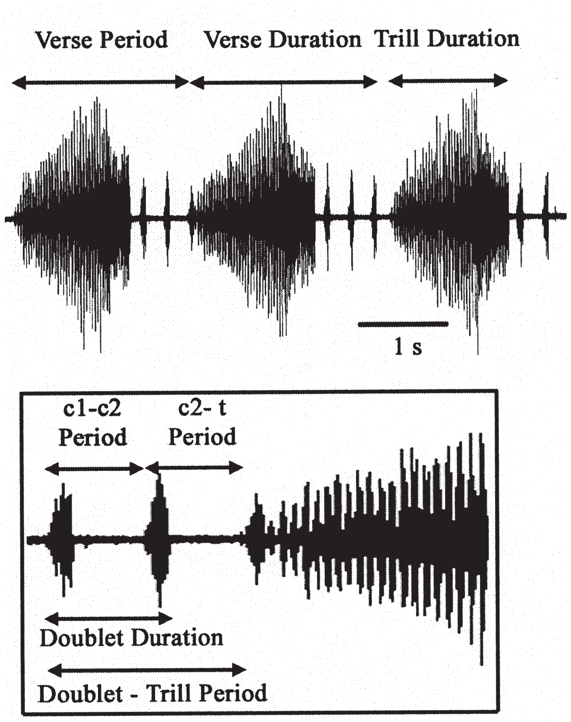


Figure 6. Oscillogram of the call of the song type *Two Part Caller*. Inset shows a magnified view of the chirps.

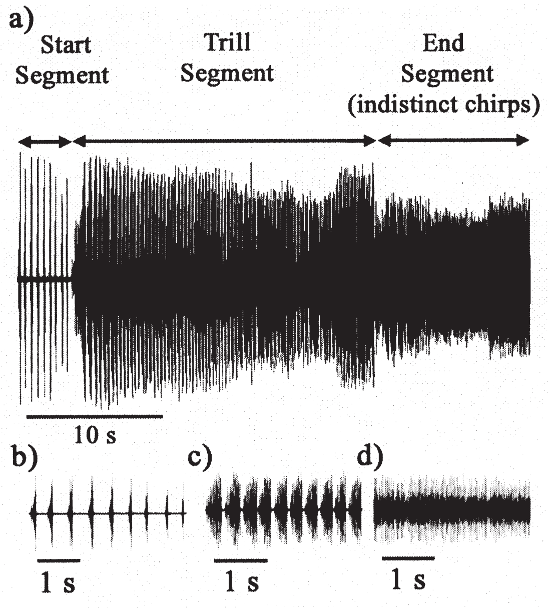


Figure 7. Oscillograms of the call of the song type *Helicopter*: a) A single verse. b) Start segment. c) Trill segment. d) End segment of the verse.

12 syllables structured similar to those of *Chirper* with varying periods (mean period = 9 ± 0.6 ms) (Table 2d). The second segment ("Trill") had chirps with longer durations and shorter periods (Figure 7c, Table 1d). In the third segment ("End") the chirps merged into each other and were not distinguishable (Figure 7d). This segment consisted only of syllables. These syllables had different periods (mean = 10.3 ± 0.7 ms) (Table 2d) and alternated between the two syllable types. Successive syllables of a syllable type did not increase in amplitude and duration in this segment.

The Trill segment of the call was divided into three equal and consecutive parts for analysis. The mean periods and durations of the component chirps of these parts were compared. The mean duration of the chirps decreased significantly in the second and third parts of the trill (Figure 8a, $P < 0.001$ and $P = 0.001$ respectively). The mean period of the chirps in the first part of the trill was seen to be significantly greater than those of the chirps in the second and third parts ($P < 0.001$ and $P = 0.001$ respectively), which were not significantly different from each other ($P = 0.9$) indicating that the chirps accelerate in the initial one-third of the trill (Figure 8b).

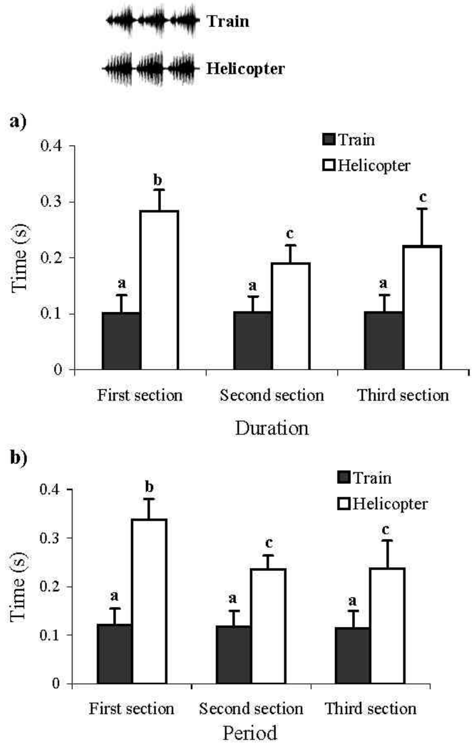


Figure 8. Comparison of the mean a) durations and b) periods of chirps in the three equal consecutive parts of the first 17 s of the trills of the species *Helicopter* and *Train*. Different letters indicate significantly different values (a = 0.05).

5. Song Type *Train*

The call consisted of repeated verses each consisting of three segments. The first or "start" segment consisted of repeated sections, each consisting of discontinuous chirps followed by bursts of indistinct chirps (Figure 9a). The discontinuous chirps consisted of 2 syllables each (Table 2e), one of each syllable type. The chirps in the bursts increased in amplitude until the end of the burst. The second or "middle" segment began with very short chirps (Figure 9b, Table 1e) that appeared to combine together to form longer chirps after approximately 5 seconds. The third or "trill" segment was comprised of these longer chirps and lasted for more than a minute (Figure 9c). The

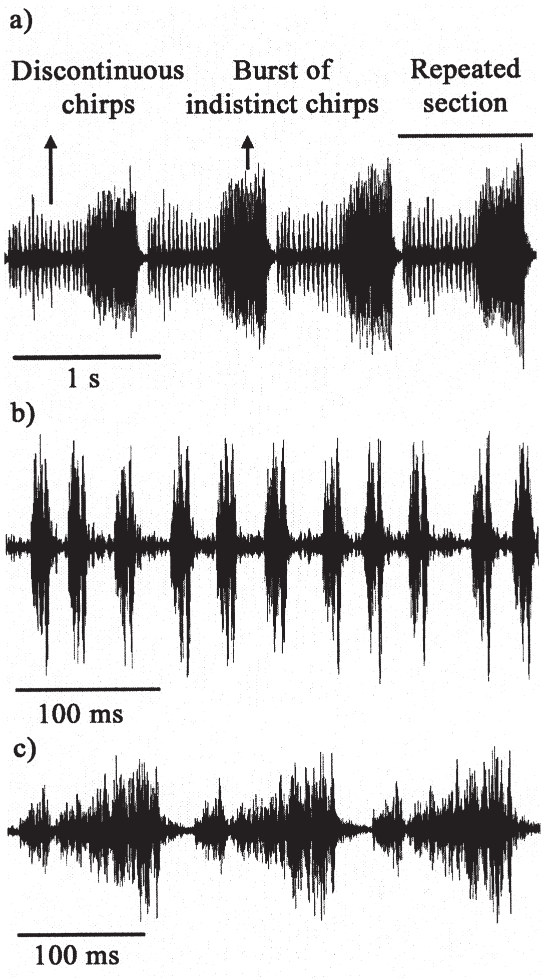


Figure 9. Oscillograms of the call of the song type *Train*: a) Starting segment. b) Middle segment. c) Trill segment.

component chirps were comprised of about 9 syllables. The syllables differed in period (mean period = 10.3 ± 2.7 ms; Table 2e) and alternated between the two syllable types. The component chirps remained distinct until the end of the trill.

In order to examine if the rate of the chirps comprising the trill increased during the course of the trill, we compared the rates of chirps in three equal and consecutive parts of the trill segment. Each of these segments was 5.7 seconds long (one-third the mean length of the *Helicopter* trill, Table 1d). This length was taken, as there were very few recordings of complete trills of *Train*. Both the mean durations and periods of the chirps in the three parts of the trill were not significantly different from each other (Figure 8, comparisons of first part-second part, second part-third part and third part-first part: $P = 0.6, 0.4, 0.8$ respectively for durations, $P = 0.1, 0.7, 0.2$ respectively for periods) indicating that the component chirps do not accelerate during the first 17 seconds of the trill (Figure 8b).

Comparison of similar song features across different song types

The more complex calls could, in principle, have evolved by a process of removing, combining or adding elementary modular units (such as chirps or doublets of chirps) as suggested by Otte (1992). For example, the song of *Two Part Caller* could have arisen by "adding" the doublet of *Double Chirper* after the trill. In order to examine if this was the case, we compared component elements ("units") of the different song types to see if they were similar. As the syllables varied in duration and period even within a chirp of a song type, no meaningful unit could be defined for the syllables. This analysis was therefore performed only at the chirp level.

Both chirp duration and period were found to be significantly different across all the song types (one-way ANOVA, $P < .001$ in each case). Specific comparisons were therefore made between the song types to see how they differed:

(a) Comparison between the song types *Chirper* and *Double Chirper*
The mean duration of the chirps of *Chirper* was significantly greater than the mean duration of either chirp of the doublet of *Double Chirper* ($P < 0.0001$ in both cases) and significantly less than the mean duration of the entire doublet ($P < 0.0001$) (Figure 5a). The mean period of the chirps of *Chirper* was significantly greater than the mean period of any of the components of the song of *Double Chirper* ($P < 0.0001$ in all cases) (Figure 5b).

(b) Comparison between the song types *Chirper* and *Two Part Caller*
The mean chirp duration of *Chirper* was significantly greater than the mean duration of either of the two chirps following the trill of *Two Part*

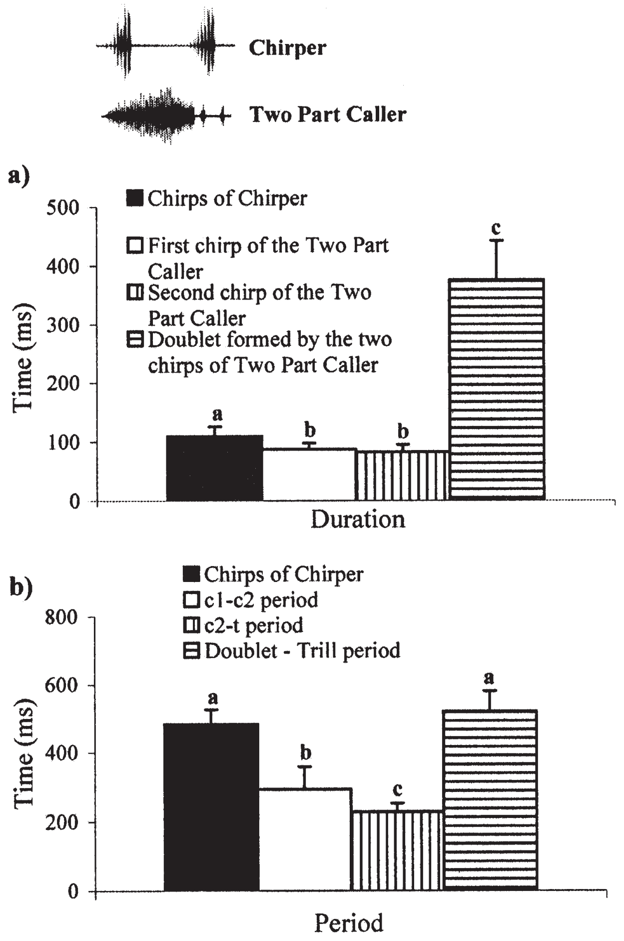


Figure 10. Comparison of mean a) durations and b) periods of the songs of *Chirper* and *Two Part Caller*. Different letters indicate significantly different values (a = 0.05).

Caller (first chirp $P = 0.003$, second chirp $P < 0.001$). The mean chirp period of *Chirper* was greater than the c1-c2 period and the c2-t period of the *Two Part Caller* (Figure 10b, $P < 0.0001$ in both cases). The "doublet" formed by the two chirps after the trill, however, had a significantly longer mean duration ($P < 0.0001$) but not period ($P = .12$) than that of the chirps of the song type *Chirper* (Figure 10).

(c) Comparison between the song types *Double Chirper* and *Two Part Caller*

The values of the song features were compared considering 1) the two chirps of the trill of *Two Part Caller* as a "doublet" and 2) separately for each of the chirps. All mean period and duration values (for the doublets and for each of the chirps) were significantly greater ($P <$

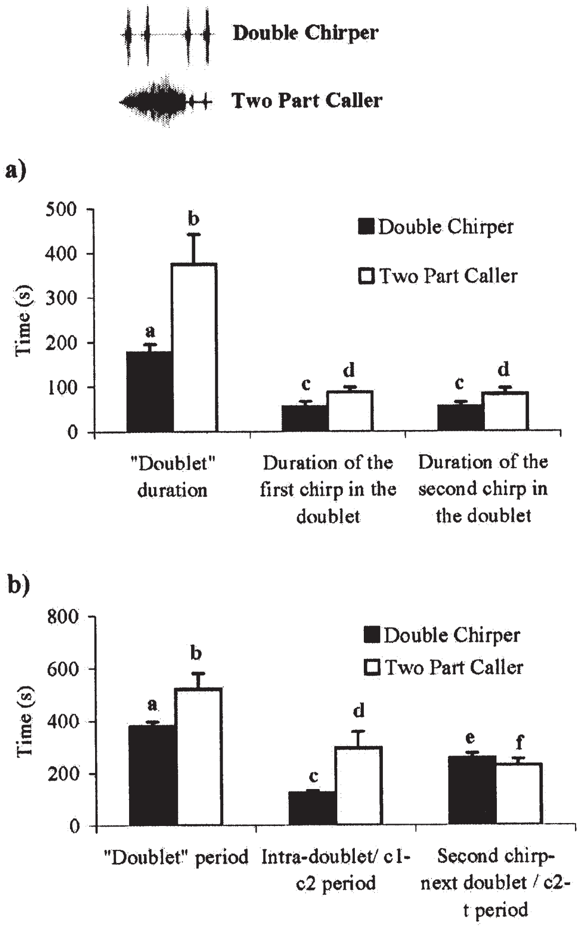


Figure 11. Comparison of mean a) durations and b) periods of the doublets of the song type *Double Chirper* and the two chirps following the trill of *Two Part Caller*. Different letters indicate significantly different values (a = 0.05).

0.0001 in all cases) for the song type *Two Part Caller* except for the second chirp period (time from the onset of the second chirp to the onset of the next doublet in the *Double Chirper*) which was significantly less ($P < 0.0001$) than the c2-t period of the *Two Part Caller* (Figure 11).

(d) Comparison between the species *Helicopter* and *Train*

The chirps forming the trills of *Helicopter* had both significantly greater mean durations ($P < 0.001$ for all three parts of the trill) and significantly greater mean periods ($P < 0.0001$ for all three parts of the trill) than the chirps forming the trills of *Train* (Figure 8). This was true for all three parts of the first 17 seconds of the trills of both song types.

Despite having similar syllable types, the songs of the five song types differed in the way these syllables were structured to form the component elements of the song. Furthermore, the component elements of the songs of the five song types differed significantly from each other in their durations and periods. Thus the songs of the five song types were found to be distinct in both macro and fine temporal features.

Morphological analysis

The individuals were typically brown or green in colour. There was variation in colour within every song type. Individuals could not be classified to a particular song type by visual examination (Figure 12). The sound producing apparatus was also strikingly similar between individuals of the five song types (Figure 12).

In the multivariate analyses using either quantitative or qualitative morphological characters (listed in Appendix 1 along with mean values of the quantitative measurements for each song type), the *Chirper* song type formed a separate cluster. None of the other song types formed distinct clusters (Figure 13). The cluster of the *Chirper* song types remained distinct even after the removal of some characters (such as body size, file length, peg number) that we thought might be important in distinguishing it from the others. We were thus unable to find diagnostic characters that distinguished this song type from the others. This indicates that all the other song types are essentially indistinguishable morphologically, while in the *Chirper* song type the combination of many characters (not only one or two diagnostic ones) distinguishes it from the other song types.

DISCUSSION

Differentiating between closely related morphologically similar song types requires detailed quantitative data on the song and morphology of the song types. Our study provides such data for the five song types of the genus *Mecopoda* from Southern India. A comparison with data on other song types of this genus could clearly separate the animals into different groups based on song and morphology. For example, our data indicate that the species described as *Mecopoda elongata* from Malaysia (Sismondo 1990; Römer *et al*. 2002) differs from the song types described here. The most similar song type is *Chirper*. However, the mean chirp duration and period of *Chirper* are 109.2 ms and 483.3 ms respectively while the chirp duration and period of the species described from Malaysia are 200–300 ms and 1.7–2 s (Römer *et al*. 2002). Detailed analyses of song and morphology are, however, currently unavailable for several of the other Malaysian and Indonesian members of the genus *Mecopoda*.

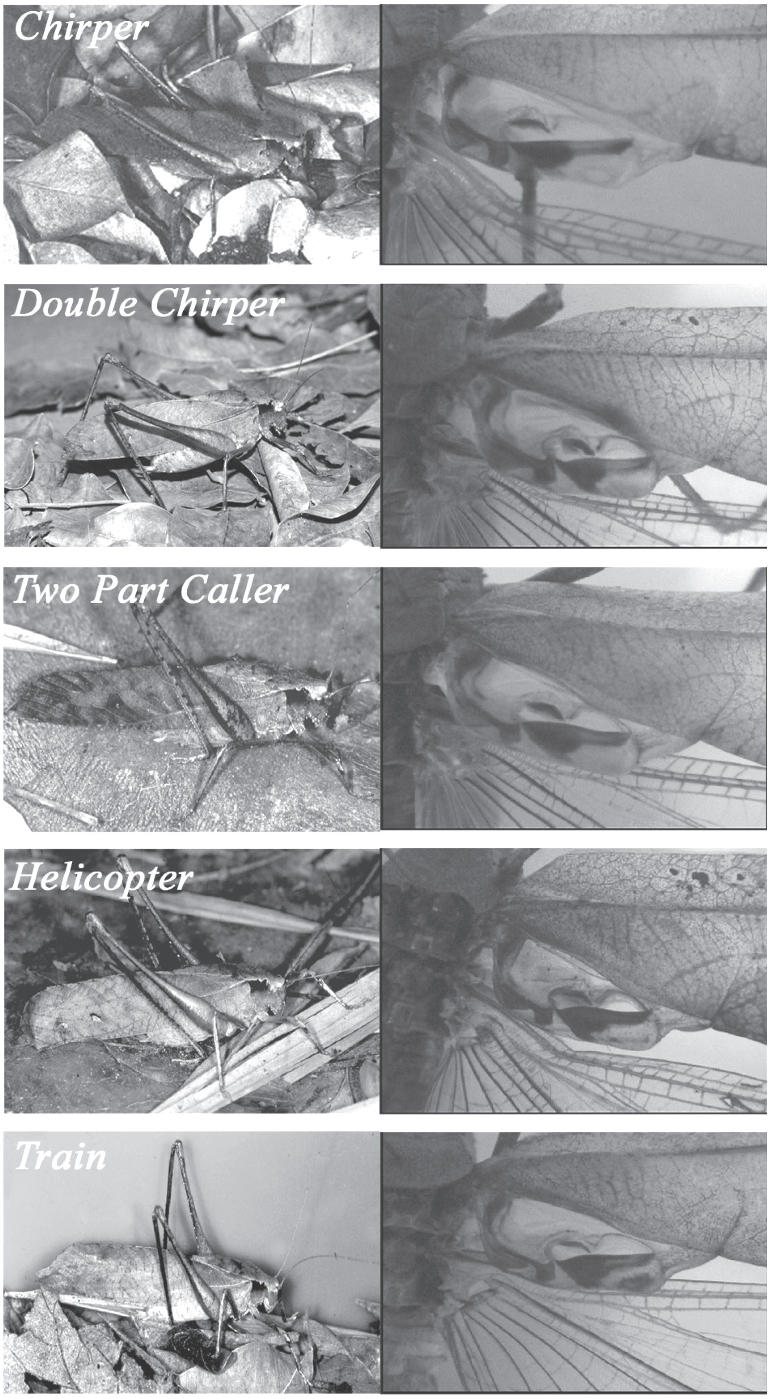
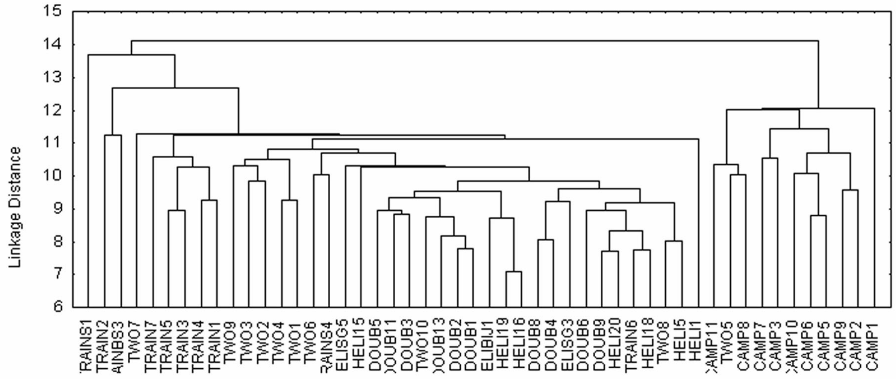
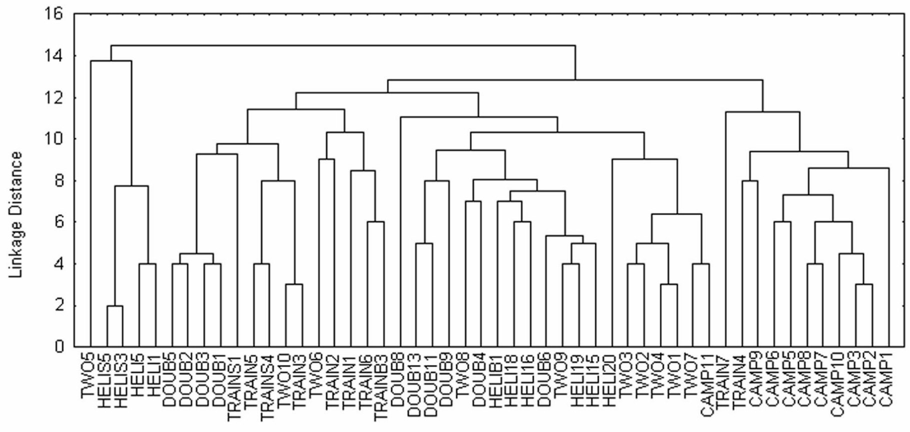


Figure 12. Representative individuals and dorsal views of the right forewing showing the mirror area of the five song types.



a) Quantitative Characters



b) Qualitative Characters

Figure 13. Phenetic clusters of the five song types of *Mecopoda* using a) quantitative morphological characters and b) qualitative morphological characters. CAMP = *Chirper*, TWO = *Two Part Caller*, DOUB = *Double Chirper*, HELI = *Helicopter*, *TRAIN* = *Train.*

Are the Mecopoda *song types cryptic species?*

The song types may either represent cryptic (sibling) species or different interbreeding song morphs of the same species. It has been seen in both crickets (Alexander 1968) and katydids (Ritchie 1996) that interbreeding between individuals of different song types produce hybrid offspring whose songs are intermediate between the songs of the two song types. Walker *et al.* (2003) add that song types in sympatry are almost definitely different species. Since the song types we have found are largely in sympatry and there are no intermediate song types, it seems unlikely that the song types described here are interbreeding. Thus they most likely are different sibling species rather than song morphs.

Sibling species are by definition morphologically cryptic (Walker 1964) and are often not classified as separate species if only morphological characters are used in the classification. They may, however, be distinguished in crickets and katydids by their distinct calling songs (*Oecanthus*: Walker 1964; *Laupala*: Otte 1994; *Ephippiger*: Ritchie 1996; *Amblycorypha*: Walker *et al.* 2003). These differences in songs could be indicators of reproductive isolation (demonstrated in Walker 1957; Hill *et al.* 1972; Ulagaraj and Walker 1973,) since the songs serve the purpose of attracting potential mates. In the genus *Laupala*, differences in song have also been shown to correspond to species boundaries inferred on the basis of mitochondrial DNA variation (Otte 1994; Shaw 1999). Thus, calling songs are usually reliable indicators of distinct species (Shaw 1999) if the song types are sympatric. Confirming this in the case of *Mecopoda* would require either demonstrating reproductive isolation (following the Biological Species Concept: Mayr 1963) due to song or chromosomal or molecular differences between the song types.

The simplest methods that one can use to test reproductive isolation are courtship and mating assays or measuring female preference for specific calling songs. In the case of our *Mecopoda* song types, this is complicated since, in addition to being morphologically identical, several of the song types are both sympatric and synchronous. It is, therefore, not possible *a priori* to unambiguously assign a particular female to any song type on the basis of external morphology. An additional method of establishing reproductive isolation would be the analysis of internal genital structures, which may reveal differences corresponding to the song types, suggesting that they are reproductively isolated.

Alternatively, species may be delineated using cytogenetic and molecular methods. Aswathnarayana & Aswath (1994) found differences in chromosomal number between individuals of the genus *Mecopoda* from India. The songs of the two chromosomal types are, however, unknown. Another method would be via a molecular phylogenetic analysis of the different song types with species being delineated on the basis of phylogenetic species concepts (de Queiroz 1998; Cracraft 2000).

Signal evolution and speciation in Mecopoda

Regardless of their taxonomic status, the striking morphological similarity of these five song types indicates that they are closely related. In addition to this, the diversity of macro-temporal patterns seen in these five song types is great, spanning a range typically seen at much higher taxonomic levels. These two facts make this a very interesting system in which to examine signal evolution and speciation. Previously studied sibling species of crickets (*Nemobius*: Alexander 1957; *Laupala*: Otte 1994) often show only a difference in chirp rate (but see *Teleogryllus* (Hill *et al.* 1972) for a counter example). Otte (1992) suggests that complex calls can evolve by changing rates and dropping or adding pulses or chirps as units. Our comparative analysis, however, indicates that the “units” (doublets or chirps) of the different song types of *Mecopoda* are all significantly different from each other in duration. While these units might still be homologous, this indicates that the evolution of complex calls cannot be fully explained in terms of changing the order or timing of fixed modular units.

The actual pattern of signal evolution in *Mecopoda* remains to be ascertained using a phylogenetic approach. As pointed out by Desutter-Grandcolas (2003) it would be necessary to use rigorous definitions of characters and statements of homology followed by a phylogenetic analysis to gain insights into the patterns of signal evolution. The patterns of signal evolution in *Mecopoda* probably reflect changes in the neural oscillators responsible for song production (Alexander 1962) since the stridulatory apparatus of these song types are very similar. The similarity of the stridulatory structures might also explain why the spectra of the different songs are similar despite the differences in temporal pattern.

The patterns of signal evolution could be the product of divergence during or after speciation. If the populations had speciated in allopatry, changes in the songs might have occurred due to genetic divergence (Mayr 1963). Furthermore, upon encountering each other subsequently, there would be selection pressure on them to evolve different signals and enable premating isolation either through reproductive character displacement or reinforcement (Wells and Henry 1998 and references therein). This could explain the diversity of songs between the song types of *Mecopoda.*

Alternatively, the differences in signals could have led to speciation. Differences in courtship signals can lead to sympatric speciation by sexual selection (Wells & Henry 1998 for lacewings; Higashi *et al*. 1999). To build a case for sympatric speciation due to signal divergence, however, it would be necessary to rule out ecological speciation (reviewed in Schluter 2001) and demonstrate reproductive isolation on the basis of song. Molecular data could also reveal whether speciation occurred at an accelerated rate, which can be the result of sexual selection (West Eberhard 1987; Pomiankowski & Iwasa 1998). A recent study (Mendelson & Shaw 2005) has shown such an accelerated rate of evolution in crickets of the genus *Laupala* that have also previously been shown to be ecologically similar (Otte 1994) and reproductively isolated due to song (Mendelson & Shaw 2002).

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APPENDIX 1

List of characters used for the cluster analysis and mean values for each quantitative character for each song type. All measurements of length and width in mm.

1. Quantitative characters (75)

S. No.	Character	Chirper Double	Double Chirper	Two Part Caller	Helicopter	Train
1	Body length	25.78	31.3	31.61	29.99	32.67
2	Head length	2.31	2.51	2.41	2.37	2.4
3	Eye to eye width	3.76	4.34	4.33	4.21	4.34
4	Eye length	1.96	2.42	2.36	2.23	2.3
5	Eye width	1.36	1.6	1.64	1.57	1.67
6	Pronotum length	6.94	7.66	8.22	7.62	8.37
7	Pronotum maximum width	6.95	7.86	7.54	7.4	8.04
8	Pronotum minimum width	3.58	4.08	4.09	3.98	4.21
9	Fastigium length	2.58	2.96	2.89	2.85	2.92
10	Scape length	1.42	1.46	1.52	1.49	1.52
11	Pedicel length	0.6	0.77	0.74	0.67	0.7
12	Frons length	2.66	3	3.17	3.12	3.04
13	Clypeus length	1.55	1.87	2.14	2.28	1.93
14	Distance between antennae	2.49	2.81	2.43	2.56	2.63
15	Length of 5th segment of maxillary palp	2.51	2.84	2.94	2.87	2.92
16	Length of 4th segment of maxillary palp	1.12	1.19	1.2	1.29	1.3
17	Length of 3rd segment of maxillary palp	1.52	1.83	1.94	1.91	2.01
18	Length of 2nd segment of maxillary palp	0.66	0.81	0.89	0.78	0.9
19	Prosternal process length	1.28	1.56	1.53	1.62	1.57
20	Prosternal process width	0.41	0.45	0.56	0.39	0.48
21	Length of anterior femur	8.44	10.47	10.92	10.38	11.81
22	Maximum width of anterior femur	1.18	1.51	1.28	1.48	1.4
23	Length of anterior tibia	9.01	10.11	10.67	9.89	11.38
24	Maximum width of anterior tibia	1.02	1.17	1.05	1.18	1.14
25	Minimum width of anterior tibia	0.65	0.76	0.62	0.74	0.73
26	Anterior tympanum length	1.51	1.75	1.66	1.69	1.71
27	Anterior tympanum width	0.65	0.75	0.66	0.72	0.73
28	Posterior tympanum length	1.45	1.74	1.74	1.67	1.78
29	Posterior tympanum width	0.58	0.71	0.71	0.73	0.72
30	No. of spines on dorsal inner anterior tibia	4.7	6.3	5.6	6.3	6
31	No. of spines on dorsal outer anterior tibia	6.2	4.3	4.2	4.2	3.8
32	No. of spines on ventral inner anterior tibia	10.3	11.3	11.5	11.2	11.2
33	No. of spines on ventral outer anterior tibia	9.7	11.8	11.9	10.9	11.6
34	No. of spines on anterior femur	1.9	2.3	2	2.7	2.4
35	Length of middle femur	11.59	12.8	13.20	12.88	14.01
36	Width of middle femur	1	1.23	1.19	1.2	1.13
37	Length of middle tibia	11.18	13.0	13.09	12.80	13.99

continued

Appendix 1 continued

S. No.	Character	Chirper Double	Double Chirper	Two Part Caller	Helicopter	Train
38	Maximum width of middle tibia	0.64	0.92	0.83	0.95	0.75
39	No. of spines on dorsal inner middle tibia	5.7	7.5	7.5	7.7	7.2
40	No. of spines on dorsal outer middle tibia	6.2	5.7	5.7	6.1	4.8
41	No. of spines on ventral inner middle tibia	11.7	12.5	12.7	12.8	11.4
42	No. of spines on ventral outer middle tibia	13.2	13.3	13.4	13.7	12.7
43	No. of spines on middle femur	0.1	0	0.5	0.1	0
44	Length of 1st tarsal segment of the middle leg	1.08	1.3	1.28	1.4	1.31
45	Length of 2nd tarsal segment of the middle leg	0.85	1.1	1.07	0.97	1.09
46	Length of 3rd tarsal segment of the middle leg	1.02	1.38	1.29	1.43	1.45
47	Length of 4th tarsal segment of the middle leg	1.32	1.51	1.55	1.36	1.46
48	Length of posterior femur	35.3	38.89	40.37	40.29	41.7
49	Maximum width of posterior femur	4.81	5.49	5.52	5.58	5.35
50	Minimum width of posterior femur	1.15	1.29	1.25	1.27	1.14
51	Length of posterior tibia	35.07	38.20	39.99	38.69	40.78
52	Maximum width of posterior tibia	0.91	1.05	1.02	1.04	0.97
53	No. of spines on dorsal inner posterior tibia	24.8	23.3	22.6	22.8	23.2
54	No. of spines on dorsal outer posterior tibia	25.1	25.4	24.5	24.8	24.8
55	No. of spines on ventral inner posterior tibia	14.3	15.2	15.2	15	15.4
56	No. of spines on ventral outer posterior tibia	15.8	16.5	16.3	16.2	14.9
57	No. of spines on posterior femur	7	10.5	8.5	10.4	11.4
58	Length of longest inner spur on posterior tibia	1.15	1.43	1.27	1.48	1.4
59	Length of longest outer spur on posterior tibia	1.05	1.23	1.17	1.13	1.08
60	Length of cerci	2.29	2.51	2.4	2.33	2.48
61	Maximum width of cerci	0.86	0.93	0.88	0.9	0.93
62	Length of forewing	46.18	50.70	52.88	50.48	53.08
63	Maximum width of forewing	10.58	11.66	12.03	12.09	13.71
64	Maximum length of harp	6.28	6.55	6.15	6.28	7.35
65	Maximum width of harp	2.64	2.59	2.58	2.49	3.11
66	Maximum length of “pocket” (wing turned over)	5.73	5.72	5.72	5.57	6.18
67	Length of file	3.94	5.3	4.51	4.62	5.47
68	Width of file	0.5	0.79	0.69	0.79	0.64
69	Peg number	93.3	87.7	90.2	84.9	100.8

continued

Appendix 1 continued

S. No.	Character	Chirper Double	Double Chirper	Two Part Caller	Helicopter	Train
70	No. of branches of the subcostal vein of the elytra	9.1	8.9	8.7	8.7	8.671
71	Length of hindwing	43.9	45.17	50.56	46.51	49.61
72	Maximum width of hindwing	18.49	21.61	21.77	21.18	22.62
73	No. of hardened veins on hindwing	13.5	14.5	14.1	14.5	13.7
74	Length of subgenital plate	4.76	5.41	5.44	5.14	5.5
75	Width of subgenital plate at base	2.71	2.55	2.54	2.47	2.72

2. Qualitative Characters (61)

S. No.	Character
1	Curve of anterior margin of pronotum
2	Curve of posterior margin of pronotum
3	Widening of pronotum
4	Split prozonum
5	Curve of line splitting prozonum
6	Mid dorsal line
7	V on 2nd segment of prozonum
8	Patches at the end of the V
9	Brown dots at the base of the V
10	Coloration on metazonum
11	Dorsolateral darkening of pronotum
12	Head colour
13	Widening of fastigium
14	Colour of dorsal fastigium
15	Curve of fastigial edge
16	Parallel brown lines from fastigium to pronotum
17	Colour of anterior fastigium
18	Face orientation
19	Curve of frons-clypeal suture
20	Coloration of maxillary palps
21	Light coloration on joints of maxillary palps
22	Eye shape
23	Eye colour
24	Colour of band under the eye
25	Colour of top rim of eye
26	Scape colour
27	Pedicel colour
28	Darkening on the base of antennal segments
29	Colour of labrum
30	Coloration from eyes to clypeum

continued

Appendix 1 continued

S. No.	Character
31	Coloration from ends of fastigium to clypeum
32	Body colour
33	Shape of prosternal process
34	Colour of prosternal process
35	Dorsal ridge on abdomen
36	Ventral row of abdominal spots
37	Central line on ventral abdomen
38	Cerci shape
39	Cerci colour
40	Subgenital plate shape
41	Subgenital plate colour
42	Presence of spots on anterior margin of forewing
43	Colour of spines on anterior leg
44	Position of spines on anterior tibia
45	Coloration of anterior tibia
46	Presence of spots on ventral side of anterior tibia
47	Presence of spines on anterior femur
48	Coloration of anterior femur
49	Colour of spines on middle leg
50	Position of spines on middle tibia
51	Coloration of middle tibia
52	Presence of spots on ventral side of middle tibia
53	Presence of spines on middle femur
54	Coloration of middle femur
55	Colour of spines on posterior leg
56	Position of spines on posterior tibia
57	Coloration of posterior tibia
58	Presence of spots on ventral side of posterior tibia
59	Presence of spines on posterior femur
60	Coloration of posterior femur
61	Presence of striations on femur