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Vertical stratification in an acoustically communicating ensiferan assemblage of a tropical evergreen forest in southern India

Swati Diwakar and Rohini Balakrishnan[1]

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India

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Abstract: This study provides the first quantitative description of vertical stratification in calling heights of ensiferan species constituting most of the dry-season nocturnal acoustic community of an evergreen forest in Kudremukh National Park in south-west India. Calling heights of an average of 26 individuals of each of the 20 ensiferan species were measured and subjected to an analysis of variance to test for differences in mean calling height between species and a cluster analysis to check for the presence of discontinuous calling height layers. There were significant differences in mean calling heights between species. Calling heights of different gryllid and tettigoniid species ranged from the ground to the canopy. More gryllid than tettigoniid species occupied the ground and herb layer. Our study revealed vertical stratification of calling heights, with discrete layers corresponding to the canopy, understorey and the ground layer. These clusters emerged from the raw data of calling heights of individuals without a priori distinction of layers. We found no significant correlation between the calling heights of species and call features, including mean dominant frequency of narrow band calls, mean syllable rate and mean duty cycle.

Key Words: Acoustic, crickets, Ensifera, katydids, Kudremukh

INTRODUCTION

The suborder Ensifera in the order Orthoptera consists of superfamilies Grylloidea (crickets), Tettigonioidea (katydids) and Gryllacridoidea (raspy crickets, king crickets and wetas) (Rentz 1996). They are mainly nocturnal and use acoustic signals for long-distance communication. Males produce calling songs that attract females of their species. Each species produces a stereotyped call with specific spectral and temporal features that are used by the female for species recognition (Otte 1992 and references therein).

In tropical forests, a large number of species (bird, frog, mammal and insect) broadcast signals in the same acoustic space and time, thereby increasing the probability of acoustic interference due to overlap of frequencies and masking of temporal patterns (Römer 1993, Römer *et al.* 1989). The ensemble of acoustically communicating animals can thus be considered as a community that competes for acoustic broadcast channels and time (Riede 1993).

The use of different dominant frequencies and temporal patterns of calls has been suggested as a mechanism to reduce acoustic interference (Duellman & Pyles 1983, Hödl 1977). Calls of sympatric species have been found to be more different from each other than allopatric species (Drewry & Rand 1983). Also, sympatric species with similar calls were found to have different calling sites or seasons. Separation in either horizontal or vertical space has also been suggested as a strategy to avoid acoustic interference (Hödl 1977, Sueur 2002).

Vertical stratification is the distribution or preference of organisms for limited strata within three-dimensional space (Basset *et al.* 2003). The vertical distribution of arthropods in tropical forests has been investigated in detail in various groups, including insects such as butterflies (DeVries *et al.* 1997), fruit flies (Tanabe 2002), ants (Brühl *et al.* 1998), spiders (Sorensen 2003) and herbivorous insects (Basset *et al.* 1992, 2001). These studies have demonstrated vertical stratification in the abundance and diversity of arthropod species, especially in the canopy and understorey. Among calling animals, calling height preferences have been reported in cicadas (Sueur 2002), frogs (Hödl 1977, Lamb 1987, Ptacek 1992) and crickets (Nischk & Otte 2000) but these are

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[1] Corresponding author. Email: rohini@ces.iisc.ernet.in

preliminary and qualitative. To our knowledge there have been no rigorous quantitative studies on the stratification of the ensiferan fauna in tropical forests.

We have studied vertical stratification in an acoustically communicating ensiferan assemblage in two ways. In the first approach, we have tested the null hypothesis of no differences in calling heights between species in the assemblage. In the second approach, we have examined whether discontinuous layers emerge from the raw data of calling heights of the species, suggesting the presence of discrete strata. Strata were not defined a priori.

It has been speculated that calling heights of species will be influenced by different call features such as dominant frequency, syllable repetition rate and call duty cycle but only a few studies on a single genus of tree frogs have studied the relation between perch height and call variables (Asquith *et al*. 1988, Höbel & Gerhardt 2003). Call variables were not found to be correlated with perch height in these studies. To our knowledge, no study has investigated the relation between call variables and calling heights of ensiferans in an assemblage.

The aim of this paper was (1) to determine whether an acoustically communicating assemblage of ensiferan species exhibited vertical stratification of calling sites and (2) to examine whether the species-specific call features were related to the calling heights of species in the assemblage.

METHODS

Study site and period

The study was carried out in the Kudremukh National Park (KNP) located in the Western Ghats in Karnataka state in southern India. The KNP (600 km^2) is located between 13°01′ to 13°29′ N latitude and 75°01′ and 75°25′ E longitude. The altitude ranges from 100 m to 1700 m asl. The park receives an average annual rainfall of 4000 mm. The vegetation in the park consists predominantly of evergreen and mixed semi-evergreen forests. The national park also has plantations in the peripheral lowland area and *sholas* (high-altitude evergreen forests) and grasslands in the higher altitudes. There is no quantitative study on plant species composition and forest structure in the National Park. Preliminary data show that the average height till first branching of trees (which are greater than 25 cm in girth at breast height) is 12 m. The average height of trees is approximately 25–30 m. The forest consists of evergreen tree species such as *Poeciloneuron indicum*, *Artocarpus hirsutus*, *Dimocarpus longan*, *Alstonia scholaris*, *Syzygium cumini* and *Hopea parviflora* (nomenclature follows Saldanha 1984). The ground is typically covered with leaf litter and there are no grasses. The herb layer consists of small tree saplings and herbs and is typically less than 0.5 m in height. Shrubs and tree saplings range from about 1–8 m in height and constitute the understorey. The study was carried out after the monsoon season between October and March 2003–2006.

Vertical stratification

Calling individuals were tracked and located by ear in the forest. Animals calling from the understorey were tracked by climbing a 2-m ladder and the calling height of individuals from the ground was measured using a measuring tape. Heights of the animals calling from the canopy were measured by first localizing the tree from which the animal was calling. A field assistant with excellent tree-climbing and insect-localizing skills then climbed the tree and located the animal. The field assistant kept one end of the measuring tape as close to the animal as possible and dropped the other end to the ground so that the exact height of the calling insect from the ground could be measured. In some cases where the animals were calling on leaves of a branch in either a horizontal or vertical direction that was not possible to manually access, a graduated long pole with one end of the measuring tape tied to it was used to reach close to the position where the call of the animal could be heard loudest. The other end of the measuring tape was dropped from there and measurements were taken.

The calling height data of species were checked for equality of variances using Bartlett chi–square test ($\chi^2 = 679$, $P < 0.01$) (Sokal & Rohlf 1981) which revealed inhomogeneity of variances. Hence, calling height data were $\log_{10}(x + 1)$-transformed to correct for inequality of variances in the data (Sokal & Rohlf 1981). Homogeneity of variances on the log-transformed data was tested (Bartlett chi–square test $\chi^2 = 15.9$, $P = 0.39$). The mean and standard deviation of individual calling heights were calculated for each species. Differences between species in mean calling height were examined using a one-way ANOVA on the log-transformed calling height data followed by post hoc pair-wise comparisons using Tukey's HSD test (Zar 1984). The calling height data were also examined using unweighted pair-group average (UPGMA) cluster analysis of a Euclidean distance matrix (Manly 1986). All statistical analyses were carried out using the software Statistica (1999, Statsoft Inc., USA).

Calling height and call features

Calling crickets and katydids were tracked and located by ear in the field. Calls of individual males were recorded in the evening between 19h00 and 22h00. Recordings were made using either a Sony stereo microphone

(ECM-MS957, frequency response: 50–18 000 Hz) and stereo cassette recorder (Sony WM-D6 C Professional Walkman) or an ultra sound detector (D 980, Pettersson Elektronik AB, Sweden, frequency range: 2–200 kHz) and acquired on a laptop computer (IBM® ThinkPad® R32) using a data acquisition card (DAS 16/330, Measurement Computing) at a sampling rate of 200 kHz. In the former case, sound recordings were sampled via an analog-digital converter (Creative Sound Blaster A/D Card) at a sampling rate of 44 kHz.

The ambient temperature was measured after each recording with a thermometer (Kestrel 3000 Pocket Weather Station). After call recordings, the animals were captured and preserved in 70% alcohol for taxonomic work. Collected specimens were identified using the taxonomic keys developed by Chopard (1969) for gryllids and Brunner von Wattenwyl (1888), Beier (1962) and Rentz (1996) for tettigoniids to the genus level. Two call types were identified only up to the subfamily level and the temporary names ‘Whiner’ (Gryllidae: Podoscirtinae) and ‘15 kHz’ (Tettigoniidae: Phaneropterinae) have been used. We have not been able to verify species identity due to problems of accessing type specimens and hence species names have been avoided. We are however confident that each of the calls described constitute a single species, based on detailed acoustic and morphological analysis (Diwakar & Balakrishnan in press).

Spectral analysis was performed using the signal processing software Spectra Plus Professional (1994, Version 3.0, Pioneer Hill Software, Poulsbo, WA). The bandwidth of the frequency spectrum was measured at 20 dB below the frequency at peak amplitude. Temporal pattern analysis was performed using a custom-built program (Chandra Sekhar, ECE, IISc) in Matlab (1997, Version 5.1.0.421, The Mathworks Inc., Natick, MA) and the following call characters were measured: call duration, call period, syllable duration and syllable period. Each call feature was regressed against temperature. If a feature of a call showed a significant change with temperature, it was regressed to 24 °C (the temperature at which the calls of most other species were recorded) for comparisons between species. Means and standard errors were calculated for call features of each species.

The distributions of three call features, namely dominant frequency, syllable repetition rate (1/syllable period) and duty cycle (call duration/call period) were examined for normality using a Kolmogorov–Smirnov test and found to be significantly different from normal ($d = 0.2$, $P < 0.01$, $d = 0.2$, $P < 0.01$ and $d = 0.22$, $P < 0.01$ respectively). The data were $\log_{10}$-transformed and then tested for normality using the same test ($d = 0.11$, $P < 0.1$, $d = 0.1$, $P < 0.2$ and $d = 0.07$, $P > 0.2$ for dominant frequency, syllable repetition rate and duty cycle respectively) and found to be normal. Means of log-transformed calling heights of species were correlated with the log-transformed mean dominant frequency of the narrow band calls (bandwidth < 2 kHz), mean syllable repetition rate and mean duty cycle using pair-wise Pearson correlations. Linear regression was performed to obtain the line of best fit (Gravetter & Wallnau 2004).

Table 1. Taxonomic affinities of species constituting the acoustically communicating ensiferan assemblage of Kudremukh.

- Grylloidea
  - Gryllidae
    - Gryllinae
      - *Callogryllus* sp.
      - *Scapsipedus* sp.
    - Landrevinae
      - *Landreva* sp.
    - Sclerogryllinae
      - *Sclerogryllus* sp.
    - Itarinae
      - *Gryllitara* sp.
    - Phaloriinae
      - *Phaloria* sp.
    - Oecanthinae
      - *Xabea* sp.
    - Podoscirtinae
      - ‘Whiner’
  - Mogoplistidae
    - Mogoplistinae
      - *Ornebius* sp.
      - *Micrornebius* sp.
- Tettigonioidea
  - Tettigoniidae
    - Pseudophyllinae
      - *Onomarchus* sp.
      - *Phyllomimus* sp.
      - *Brochopeplus* sp.
      - *Pirmeda* sp.
    - Phaneropterinae
      - *Elimaea* sp.
      - ‘15 kHz’
    - Mecopodinae
      - *Mecopoda* ‘Helicopter’
      - *Mecopoda* ‘Two-part’
      - *Mecopoda* ‘Train’
- Gryllacridoidea
  - Anostostomatidae
    - *Gryllacropsis* sp.

RESULTS

Description of the acoustic community

The calls of the 20 ensiferan species constituting the nocturnal acoustic community of Kudremukh National Park have already been described (Diwakar & Balakrishnan in press, Nityananda & Balakrishnan 2006). Of the 20 species, 10 belonged to the superfamily Grylloidea and had narrow band calls with dominant frequencies ranging from 3 to 7 kHz (Table 1). Each genus was represented by one species. The superfamily Tettigonioidea was represented by nine species (Table 1). All species except *Mecopoda* belonged to different genera. Three song types belonging to the genus *Mecopoda* have been given informal names ‘Two part’, ‘Helicopter’ and ‘Train’ based on their call structure (Nityananda & Balakrishnan 2006). The superfamily Gryllacridoidea was represented by one species belonging to the genus *Gryllacropsis* (Table 1, Diwakar & Balakrishnan 2006). Four of the tettigoniid species had narrow band calls and the rest were broadband callers with bandwidths ranging from 2 to 70 kHz. A spectrogram of the ambient noise recordings made during the peak calling time of ensiferans

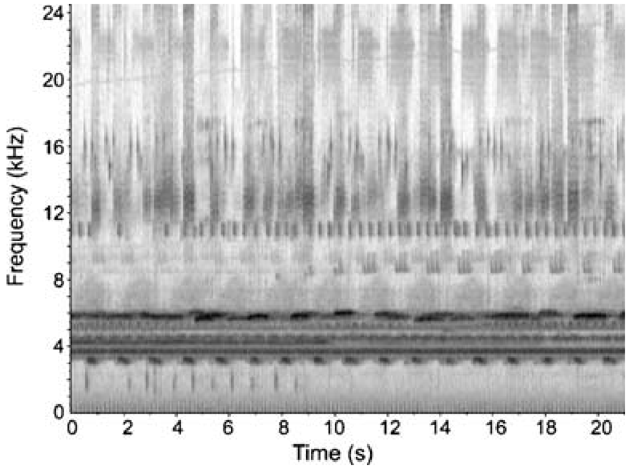

Figure 1. Spectrogram of the ambient noise recording in the evergreen forest showing the frequencies and temporal patterns of different ensiferan species calling at the same time. Temporal patterns of *Gryllacropsis* sp. (1–3 kHz), *Onomarchus* sp. (3 kHz), 'Whiner' (5.9 kHz), *Phyllomimus* sp. (9 kHz) and single and double clicks of '15 kHz' can be seen. The frequency band between 12 and 30 kHz is smeared by individuals of *Pirmeda* sp.

is shown (Figure 1). There was a high overlap of call frequencies and masking of temporal patterns between 3 and 7 kHz.

Calling height stratification

The mean calling height of species varied from the ground (0 m) in *Callogryllus* sp., *Scapsipedus* sp., *Scleropterus* sp. and *Micrornebius* sp. to 13 m in *Xabea* sp. and *Onomarchus* sp. in the canopy (Figure 2). There were significant differences in mean calling height between species (one-way ANOVA, $F = 206$, $P < 0.01$). Post hoc pairwise comparisons of the means revealed different groups (horizontal bars in Figure 2) of animals based on average calling height.

The species calling from the canopy, namely those of *Xabea*, *Onomarchus* and *Phyllomimus* formed a single group separate from the rest of the species. *Gryllacropsis* sp. with a mean calling height of 9.13 ± 3.83 m was significantly different from *Xabea* sp. in the canopy group and from species calling from the understorey and the ground (Figure 2). Species such as those of *Callogryllus*, *Scapsipedus*, *Scleropterus*, *Micrornebius*, *Gryllitara*, *Mecopoda* 'Helicopter' and *Mecopoda* 'Two part' were not significantly different from each other in calling heights and occupied the ground layer. The species of *Landreva* and *Mecopoda* 'Train' occupied the lowest part of the understorey. *Elimaea* sp., *Pirmeda* sp., 'Whiner' and '15 kHz' were predominantly understorey callers. The species of *Phaloria*, *Brochopeplus* and *Ornebius* in

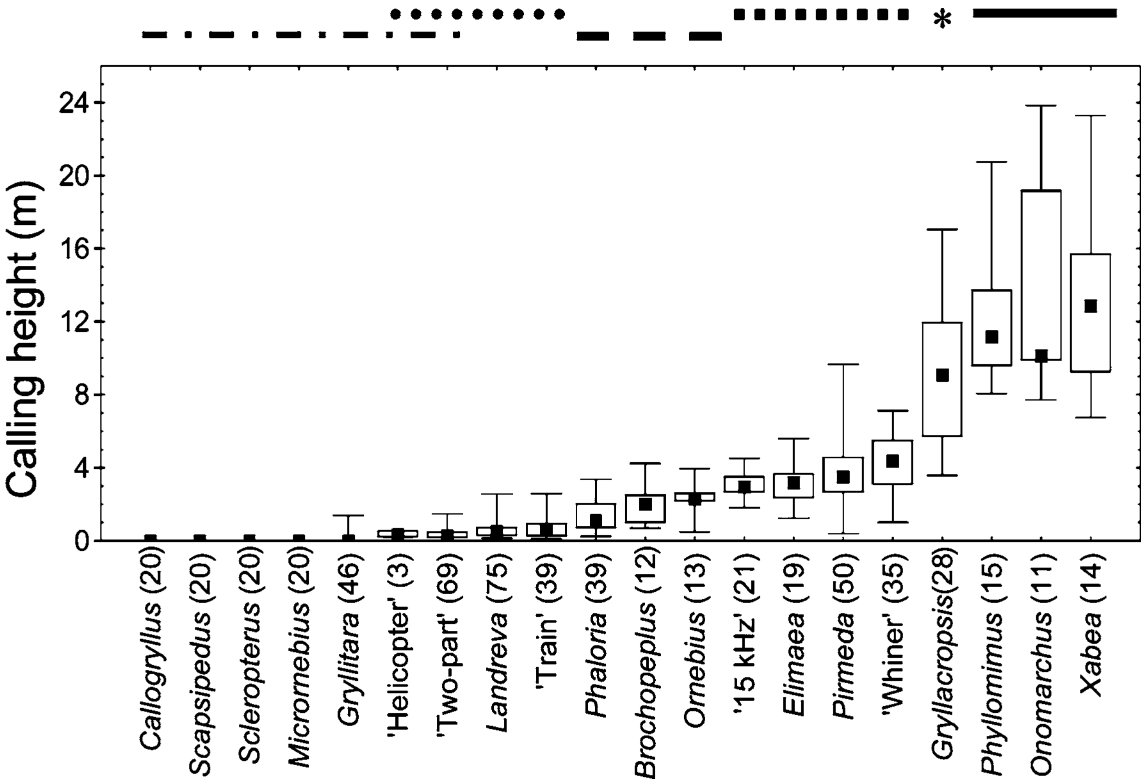

Figure 2. Calling heights of 20 ensiferan species. Solid square boxes indicate the median, empty boxes indicate the 25th and 75th percentile and whiskers show maximum and minimum values of calling sheights. Horizontal bars on the top indicate the grouping of species based on post hoc comparisons of mean heights (see text for details). Numbers in parentheses indicate number of individuals used to calculate mean calling height.

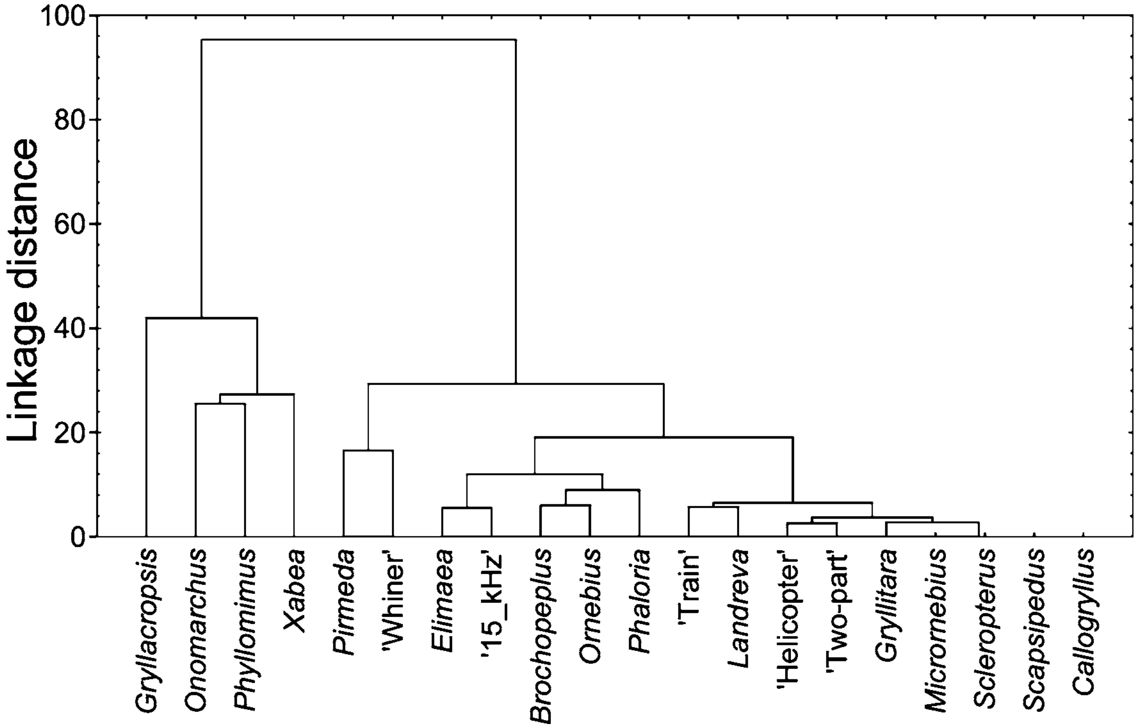

Figure 3. Dendrogram showing the grouping of ensiferan species based on calling height.

the understorey group were significantly different from 'Whiner'. The mean calling height of *Brochopeplus* sp. was significantly different from that of *Pirmeda* sp.

The cluster analysis (Figure 3) showed a similar trend of calling height stratification. The cluster diagram showed two major clusters with the canopy cluster separating out from the rest of the species. Within the canopy cluster, the *Gryllacropsis* sp. separated out. The other major cluster was formed of species calling from the understorey and the ground. The species of *Pirmeda* and 'Whiner' with mean calling heights of 3.84 ± 1.88 m and 4.26 ± 1.52 m respectively formed a separate subgroup in the understorey cluster. The other understorey subcluster consisted of species of *Elimaea* and '15 kHz' separated from species of *Brochopeplus*, *Ornebius* and *Phaloria*. The ground cluster was the same as the group that emerged from the pair-wise comparisons following the ANOVA described above (Figure 2).

Is calling height correlated with call features?

We found no significant correlation between mean calling height and dominant frequencies of 15 narrow-band calls ($r = 0.18$, $P = 0.52$, Figure 4a). There were also no significant correlations between mean calling height of species and mean syllable repetition rate ($r = 0.35$, $P = 0.14$, Figure 4b) or mean duty cycle ($r = 0.35$, $P = 0.15$, Figure 4 c).

DISCUSSION

Vertical stratification

Our study revealed vertical stratification of the calling heights of the 20 ensiferan species. Calling heights of both gryllid and tettigoniid species ranged from the ground to the canopy, although more gryllid than tettigoniid species occupied the ground and herb layer. Post hoc comparisons and cluster analysis indicated the presence of discrete calling height layers corresponding to the canopy, understorey, herb and ground layer. These clusters emerged from the raw data of calling heights of individuals of each species without a priori distinction of layers. This is in contrast to other studies on vertical stratification in arthropods and bats where baits, traps and mist nets are placed at different vertical layers, thereby demarcating the layers beforehand (Bernard 2001, DeVries *et al.* 1997, Tanabe 2002). Previous studies on crickets (Nischk & Otte 2000), cicadas (Sueur 2002) and frogs (Hödl 1977) have shown preference for the height of calling sites qualitatively. To our knowledge, this is the first study to quantitatively establish vertical stratification in calling heights in an ensiferan assemblage of an evergreen forest.

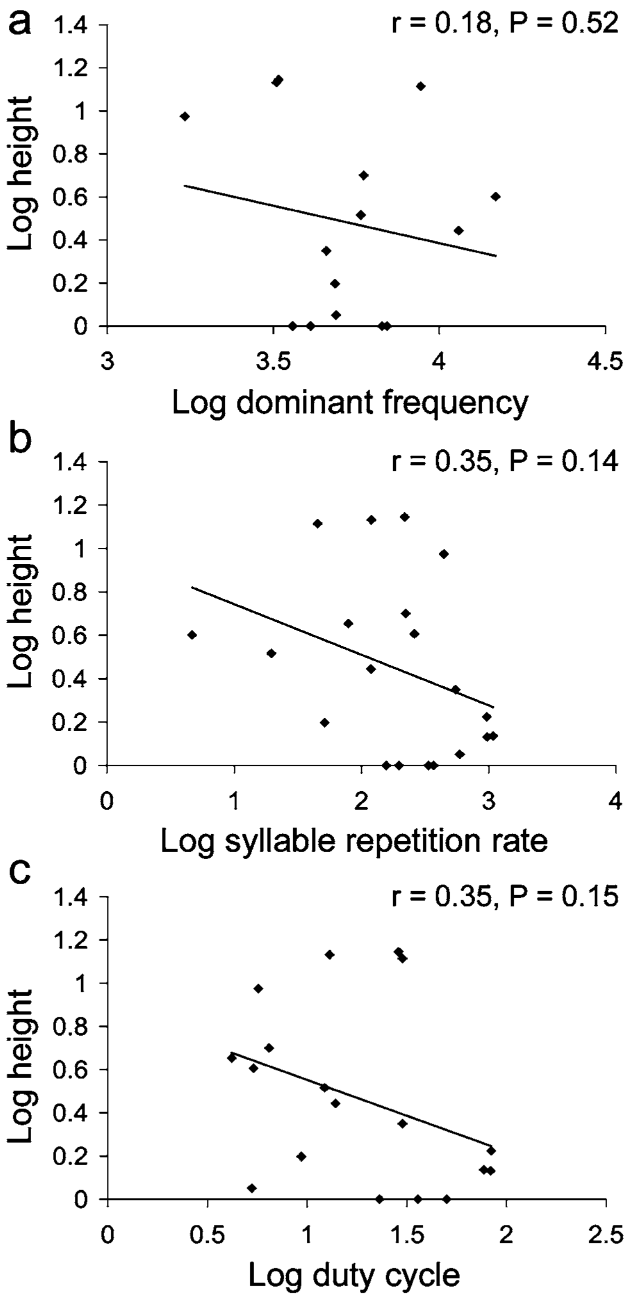

Figure 4. Correlation of mean calling height of the ensiferan species with mean dominant frequency (a), mean syllable repetition rate (syllables per second) (b) and mean duty cycle (call duration/call period) (c). Correlations were performed on log-transformed values of all variables.

Calling height and call features

In amphibians, it has been shown that species with similar dominant frequencies tend to occupy different calling sites, minimizing the risk of acoustic interference (Hödl 1977). In our study, however, we found that there was a large overlap of dominant frequencies among ensiferan species preferring identical calling heights (Figure 4a). Gryllid species such as *Callogryllus* and *Scapsipedus*, *Scleropterus* and *Micrornebius*, *Landreva* and *Gryllitara* overlapped in their call frequencies and called on or close to the ground. Similarly, in the canopy, *Xabea* sp. and *Onomarchus* sp. overlapped in song dominant frequency.

We found no correlation between the calling heights and mean dominant frequencies of the species. Since the collection of calling height data for ensiferan species involved locating calling animals by ear, we would have missed species with ultrasonic calls as well as high frequency calls in the canopy due to the frequency filtering property of forest habitats (Marten *et al.* 1977). Presence of high frequency callers in the canopy would further erode any correlations between call frequency and calling heights. Species accumulation curves suggest that the audible ensiferan community has been almost completely sampled (Diwakar & Balakrishnan in press).

Specific differences in height of calling sites could be related to different sound communication constraints. Besides inter- and intraspecific acoustic interference, acoustic communication is also constrained by the physical properties of the environment, which cause attenuation and degradation of signals (Richards & Wiley 1980). Due to frequency filtering in the habitat, low frequency signals are propagated to larger distances with less degradation (Marten & Marler 1977, Marten *et al.* 1977). Given these constraints, insects are expected to evolve signals with relatively low frequencies and occupy optimal broadcast positions (Arak & Eiriksson 1992, Paul & Walker 1979).

In our study, we found cricket species with relatively low frequency calls (3–4 kHz) occupying both the ground layer (*Callogryllus* sp. and *Scapsipedus* sp.) and the canopy (*Xabea* sp. and *Onomarchus* sp). One may speculate that these narrow-band, relatively low frequency signals may be optimal for sound transmission in the cluttered habitat of the forest floor (due to leaf litter) and the canopy (due to high leaf density). Species with high frequencies such as *Brochopeplus* sp. and '15 kHz' called mainly from vegetation in the understorey. Species with broadband calls (*Mecopoda* sp., *Pirmeda* sp. and *Elimaea* sp.) called just above the ground layer and from the understorey, suggesting that calls with higher frequencies and bandwidths may be used in the somewhat less-cluttered microhabitat of the understorey.

A study on signal transmission in two sympatric cicada species inhabiting vineyards, *Tibicina haematodes* calling from vine foliage and *Cicada orni* calling from vine trunks near the ground, showed that vertical stratification between the two species was not linked to signal propagation constraints (Sueur & Aubin 2003).

Calling height stratification in the ensiferan assemblages of tropical forests could also be due to other ecological factors such as predation by spiders, mantises, bats, birds or primates (Belwood 1990, Belwood & Morris

1987). Previous studies have shown that neotropical katydids rely on tremulatory signals, low duty cycles, pure tone and high frequency calls to avoid detection by bats (Belwood 1990). Heller (1995) has suggested differences in predation pressure by bats between the Palaeo- and Neotropics since anti-bat acoustic behaviour was less pronounced in palaeotropical pseudophyllines (false-leaf katydids). In this context, the wide range of duty cycles, presence of high duty cycle callers (such as *Mecopoda*) and the lack of correlation of duty cycle with calling height found in our study site is interesting.

Studies on acoustic transmission in different microhabitats at different heights and on predation pressure on the ensiferan species are necessary in order to gain further insight into the selective forces influencing calling height stratification.

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