

Original Article

Does acoustic adaptation drive vertical stratification? A test in a tropical cricket assemblage

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In species-rich assemblages, differential utilization of vertical space can be driven by resource availability. For animals that communicate acoustically over long distances under habitat-induced constraints, access to an effective transmission channel is a valuable resource. The acoustic adaptation hypothesis suggests that habitat acoustics imposes a selective pressure that drives the evolution of both signal structure and choice of calling sites by signalers. This predicts that species-specific signals transmit best in native habitats. In this study, we have tested the hypothesis that vertical stratification of calling heights of acoustically communicating species is driven by acoustic adaptation. This was tested in an assemblage of 12 coexisting species of crickets and katydids in a tropical wet evergreen forest. We carried out transmission experiments using natural calls at different heights from the forest floor to the canopy. We measured signal degradation using 3 different measures: total attenuation, signal-to-noise ratio (SNR), and envelope distortion. Different sets of species supported the hypothesis depending on which attribute of signal degradation was examined. The hypothesis was upheld by 5 species for attenuation and by 3 species each for SNR and envelope distortion. Only 1 species of 12 provided support for the hypothesis by all 3 measures of signal degradation. The results thus provided no overall support for acoustic adaptation as a driver of vertical stratification of coexisting cricket and katydid species. *Key words:* acoustic adaptation, attenuation, Ensifera, envelope distortion, SNR, sound transmission, temperature gradient. [*Behav Ecol*]

INTRODUCTION

Many animal species communicate over long distances in the context of mate attraction, competition, or social interaction with group members. Long-distance communication is however fraught with difficulties because signals have to propagate through a nonideal medium, the habitat, before reaching the receivers. In the case of acoustic signals, the habitat alters signals in 2 major ways. The first is attenuation or reduction in the total energy content of signals, which lowers the probability of signal detection at a distance. The second is signal distortion or change in the structure of signals in the temporal or spectral domain, making them unrecognizable (Wiley and Richards 1978, 1982). Moreover, the habitat is a noisy communication channel, and weak signals are likely to be buried in the ambient noise, making it difficult for receivers to distinguish signals from noise (Römer et al. 1989). Due to these limitations, accurate recognition and localization of degraded signals by receivers are compromised, resulting in a reduced broadcast area or active space (Wiley and Richards 1978; Klump 1996).

For species where long-distance communication influences individual fitness, it would be advantageous for a sender if advertisement signals traveled far with minimal loss of information, to be detected and recognized efficiently by “intended” receivers. In 1975, Morton suggested that habitat acoustics may exert a selection pressure that shapes the physical structure of

avian sounds. This was the first proposition of the acoustic adaptation hypothesis (AAH), which posits that attributes of the environment impose a selective pressure on long-range acoustic signals, driving signal evolution to maximize broadcast range, and the number of potential receivers (Morton 1975; Endler 1993). If acoustic adaptation is a strong enough selective force, it is expected that, over evolutionary time, the calls of animals will adapt to the constraints imposed by the environment, resulting in better transmission of signals in native habitats as opposed to non-native habitats (Morton 1975; Marten and Marler 1977; Couldridge and van Staaden 2004).

Aside from playing a role in signal evolution, habitat-induced constraints may also modify the behavior of signalers with respect to preference for calling times or positions to minimize signal distortion and attenuation (Endler 1993). Signalers may thus call only during certain “time windows” that are suitable for signal transmission (Henwood and Fabrick 1979) or may choose to call from positions that offer them transmission benefits (Arak and Eiriksson 1992; Nemeth et al. 2001). In the case of acoustically communicating animals, the optimal transmission path may be an important resource for coexisting species competing for acoustic space, and this may drive vertical stratification of calling heights. Height-dependent transmission has been examined in the context of selection of calling posts/heights in various taxa (katydids: Arak and Eiriksson 1992; birds: Marten and Marler 1977; Dabelsteen et al. 1993; Mathevon et al. 1996, 2005; frogs: Kime et al. 2000; and cicadas: Sueur and Aubin 2003). The possibility of acoustic adaptation driving vertical stratification has, however, not been examined.

Most investigations of the AAH have been carried out on larger long-ranging animals such as vertebrates and so have focused on the macrohabitat level (reviewed in Ey and

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Fischer 2009). Several insect taxa also use sound for long-distance communication (cicadas, grasshoppers, and crickets), but only 2 studies have tested the AAH in insect species (Sueur and Aubin 2003; Couldridge and van Staaden 2004). Habitats such as tropical forests have different microhabitats that differ from each other structurally. For instance, foliage density may change with height (MacArthur and Horn 1969; Wirth et al. 2001; Jain et al. 2010), which could affect the transmission properties of different layers of the forest, necessitating microhabitat level investigation of the AAH. In fact, Marten and Marler (1977) found that height influenced signal transmission more than habitat. Another obvious gap in the literature is the general absence of a community-level investigation of the AAH. Although some studies have tested the AAH in multiple species (Waser and Waser 1977; Kime et al. 2000), the species tested were either not sympatric or belonged to different communities (but see Nemeth et al. 2001; Tobias et al. 2010). Overall, there is a general paucity of studies investigating the AAH in coexisting species of an assemblage at the microhabitat level, especially in “invertebrate” taxa.

Crickets and katydids (order: Orthoptera; suborder: Ensifera) are nocturnal insects that produce sound in the context of long-distance mate attraction (Alexander 1967). One therefore expects selection pressure on them to maximize broadcast range in order to gain access to greater numbers of prospective mates, making them good systems in which to test the AAH. Kudremukh National Park in the Western Ghats of Southern India harbors a species-rich ensiferan assemblage (Diwakar and Balakrishnan 2006; Nityananda and Balakrishnan 2006; Diwakar and Balakrishnan 2007a), in which different species occupy different microhabitats (Jain and Balakrishnan 2011) and show vertical stratification with respect to calling heights (Diwakar and Balakrishnan 2007b).

In this study, we have tested the hypothesis that vertical stratification of calling heights of coexisting ensiferan species is driven by acoustic adaptation, using 3 different measures of signal degradation. If acoustic adaptation is a significant driving force of vertical stratification, then the native calling height should emerge as the best or one of the best heights for signal transmission in a majority of species in this assemblage. To our knowledge, this is the first detailed examination of the AAH at the microhabitat level, tested in a natural assemblage of coexisting insect species with respect to their vertical stratification.

MATERIALS AND METHODS

Study site and period

The study was conducted in the tropical wet evergreen forests of Kudremukh National Park (lat 13°01' to 13°29'N, long 75°01' to 75°25'E), which is situated on the windward slopes of the Western Ghats in Karnataka, India. The average annual rainfall is 4000 mm, and the elevation ranges from 50 to 1892 m asl. The forest structure in the study area consists of leaf litter-covered ground devoid of grasses, a herb layer constituted by seedlings and herbs (≤ 1 m), understory (1–8 m), and canopy (10–30 m) (Jain 2010; Jain et al. 2010). The major tree species include *Artocarpus hirsutus*, *Hopea parviflora*, *Knema attenuata*, and *Poeciloneuron indicum* (nomenclature follows Saldanha 1984, 1996). All transmission experiments were carried out in the post-monsoon dry season from December 2007 to March 2008 and December 2008 to March 2009.

Microclimatic conditions

The transmission experiments had to be carried out at a time of day that would best avoid 3 confounding factors: 1) masking

interference from calling insects during the peak calling period (6–9 PM: Diwakar and Balakrishnan 2007a), 2) early morning interference from birdsong (from 6 to 9 AM), and 3) differences in microclimatic conditions between day and night. In addition, it was important to quantify the presence of wind or temperature gradients, if any, in the forest because these have implications for sound transmission (Wiley and Richards 1978; Henwood and Fabrick 1979). Preliminary measurements showed that the temperature in the forest increased sharply in the afternoon, so 9–11 AM was selected for detailed measurements of microclimatic conditions to assess the suitability of this time window for the transmission experiments.

We measured 3 readings each of temperature, relative humidity, and wind speed at different heights in the forest (0, 0.5, 1, 2, 3, 4, 5, 6, and 8 m) using a Pocket Weather Meter (Kestrel 3000; Neilsen and Kellerman) during the morning (9, 10, and 11 AM) and evening (6, 7, and 9 PM, corresponding to the peak calling period of crickets). We made measurements thrice a month (early, mid, and late) between December and March when calling activity for most of the study species peaks. We made a total of 324 temperature readings during the day and an equal number during the night across the 4 months. We also measured relative humidity and wind speed across all time periods, months, and heights.

We pooled all the daytime temperature readings and all night temperature readings and compared the 2 groups (day and night temperatures across the 4 months) using a Mann–Whitney U test ($\alpha = 0.05$). We fitted regression lines to the height-wise temperature readings (total 72 regressions: 6 time periods/day \times 12 days) to check for the presence of any vertical temperature gradients. In addition, we calculated the variation in temperature with height for each of the 72 sets of temperature readings.

Study species, test sounds, and calling heights

We selected the calls of 12 of the 20 sympatric species of Ensifera of the assemblage of Kudremukh National Park (Diwakar and Balakrishnan 2007a) for the transmission study. These 12 species were selected so that the diversity of temporal and spectral features spanned by their calls was representative of the call features of all species in the assemblage (see Table 1, Figures 1 and 2; Diwakar and Balakrishnan 2007a). Moreover, these species also spanned the entire range of calling heights in the forest (0 to >10 m, Diwakar and Balakrishnan 2007b; Table 1) and showed strong selection for particular layers of the forest such as the ground, understory, and canopy (Jain and Balakrishnan 2011). “Call type” refers to the signal structure of each of the study species. For each of the 12 species, 1 chirp (in the case of a chirping species) or a few syllables (in the case of trilling species) was/were selected from a clean recording that had the call features representative of the species (Table 1, Diwakar 2007). The selected chirps/syllables were saved as binary files for the playback experiments.

Playback experiments

We carried out playback experiments in a flat and undisturbed patch of evergreen forest, with a representative vegetation structure (Jain et al. 2010; Jain and Balakrishnan 2011). We broadcast calls of each of the 12 species from each of 5 heights chosen to simulate sender heights: 0 m (ground), 0.5 m (lower understory), 2 m (mid understory), 4 m (upper understory), and 11 m (canopy). At every height, we rerecorded the broadcast calls at 5 distances from the speaker: 0.5 (used as the reference), 2, 4, 8, and 16 m. All calls were broadcast at 72 dB sound pressure level (SPL) (fast root mean square [RMS];

Table 1
Calling heights and call features of the 12 ensiferan species tested (adapted from Diwakar 2007)

Species	Family	Subfamily	Calling height (m)	Dominant frequency (kHz)	Bandwidth (kHz)	Call duration (seconds)	Call period (seconds)	Duty cycle (%)
<i>Mecopoda</i> “Two-part”	Tettigoniidae	Mecopodinae	0.5	n.a.	78.00	1.800	1.900	94.7
<i>Callogryllus</i> sp.	Gryllidae	Gryllinae	0	3.61	0.70	0.210	0.910	23.1
<i>Scleropterus</i> sp.	Scleropteridae	Sclerogryllinae	0	6.73	0.67	0.017	0.030	56.7
<i>Gryllitara</i> sp.	Eneopteridae	Itarinae	0	4.89	0.99	0.190	4.140	4.6
<i>Gryllacropsis</i> sp.	Anostostomatidae	–	11	1.71	2.00	0.080	1.440	5.6
<i>Landreva</i> sp.	Gryllidae	Gryllinae	0.5	4.86	0.43	0.018	0.214	8.4
“Whiner”	Eneopteridae	Podoscirtinae	4	5.91	0.42	0.940	14.680	6.4
<i>Phaloria</i> sp.	Eneopteridae	Itarinae	2	4.57	0.39	0.014	0.018	77.8
“15 kHz”	Tettigoniidae	Phaneropterinae	4	14.78	2.00	0.008	2.379	0.3
<i>Brochopeplus</i> sp.	Tettigoniidae	Pseudophyllinae	2	11.61	1.42	1.960	13.820	14.2
<i>Pirmeda</i> sp.	Tettigoniidae	Pseudophyllinae	4	13.96	16.60	0.310	7.440	4.2
<i>Onomarchus</i> sp.	Tettigoniidae	Pseudophyllinae	11	3.23	0.40	0.150	1.170	12.8

re: 2×10^{-5} N/m², measured at 0.5 m from the speaker). All SPL measurements were made using a sound level meter (Brüel & Kjær, type: Observer 2260, Brüel & Kjær 1/2 inch microphone type 4189; frequency response: 6 Hz to 20 kHz).

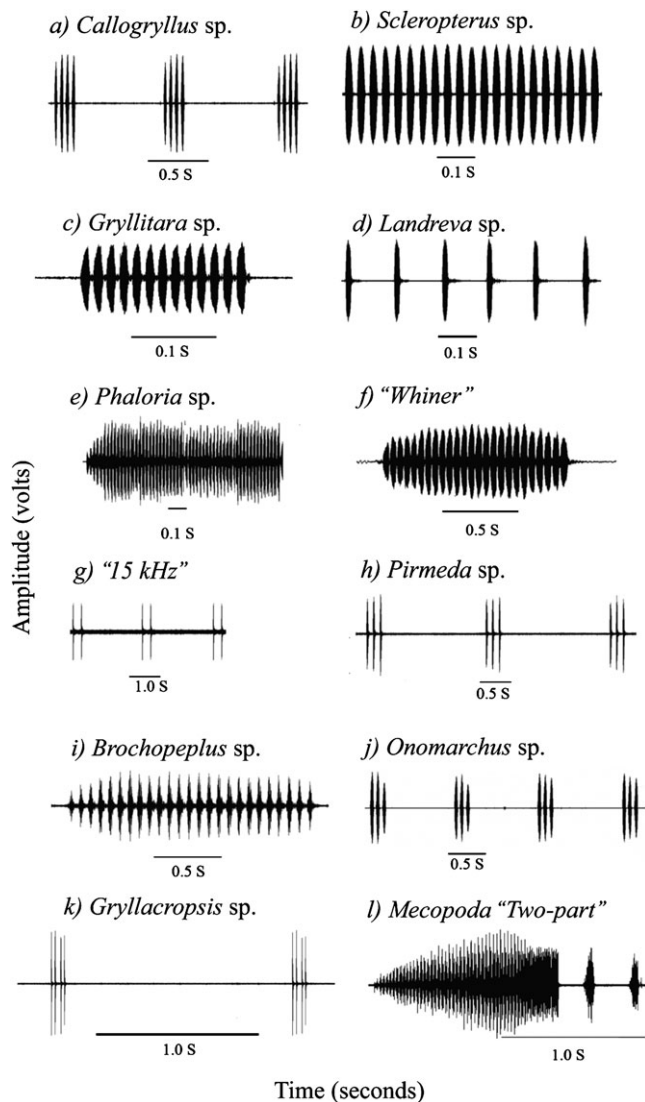


Figure 1
 Oscillograms showing temporal features of the calls of the 12 ensiferan species tested.

Output setup

The signals were played out through an Avisoft speaker (Ultrasound Scanspeak; frequency response: 1–120 kHz) via an Avisoft power amplifier. The calls were output one at a time from a laptop (IBM ThinkPad, Model 2682) using a MATLAB (version 7; The Mathworks inc., Natick, MA) interface via a D/A output card (National Instruments DAQ 6715) at a sampling rate of 200 kHz. For 9 of 12 species, we used the natural chirp period (Diwakar 2007) for the playback. Three species, namely, *Brochopeplus* sp., *Pirmeda* sp., and “Whiner” typically had very long pauses between chirps. The pause duration was reduced to 3 seconds of silence between consecutive chirps for the calls of these 3 species.

Input setup

We acquired recordings using an ultrasound detector (D 980; Pettersson Elektronik AB, Sweden, with a custom-built microphone with frequency range: 1–200 kHz) at a sampling rate of 200 kHz using the software Labview (version 6.1). The signals were acquired directly from the preamplifier output. In the canopy, for ease of movement, we used a Marantz solid state recorder (type PMD 671) and a Sennheiser Microphone (type ME-67, 40 Hz–20 kHz) to record calls with low frequency and narrow bandwidth (<10 kHz). For the high frequency, broadband calls we used the same setup as at any other height. We digitized the single channel input on to a laptop computer (IBM ThinkPad, Model 1830) using a data acquisition card (DAS 16/380, Measurement Computing; sampling rate 330 kHz) in binary format, which was later converted to .wav format using MATLAB.

The height of the speaker was the same as that of the recorder, simulating a situation where the sender and receiver are at the same height. This is based on ad libitum observations in the field, where receivers (female crickets) were always found at approximately the same heights as senders (conspecific males).

Recordings and SPL measurements

At each height, we made recordings consisting of at least 10 chirps at progressively greater distances from the speaker (0.5, 2, 4, 8, and 16 m). This sequence was repeated thrice for every height–distance combination to get a $5 \times 5 \times 12 \times 3$ factorial design (heights \times distances \times species \times replicates). Following the same protocol, at every recording height–distance combination, we made fast RMS SPL measurements using the Brüel & Kjær sound level meter (Observer 2260). For narrow bandwidth calls, a one-third octave filter was used, with the center frequency close to the carrier frequency of the call being played out. For broadband calls, we made all-pass SPL measurements, with a 500 Hz high-pass filter. Such a protocol

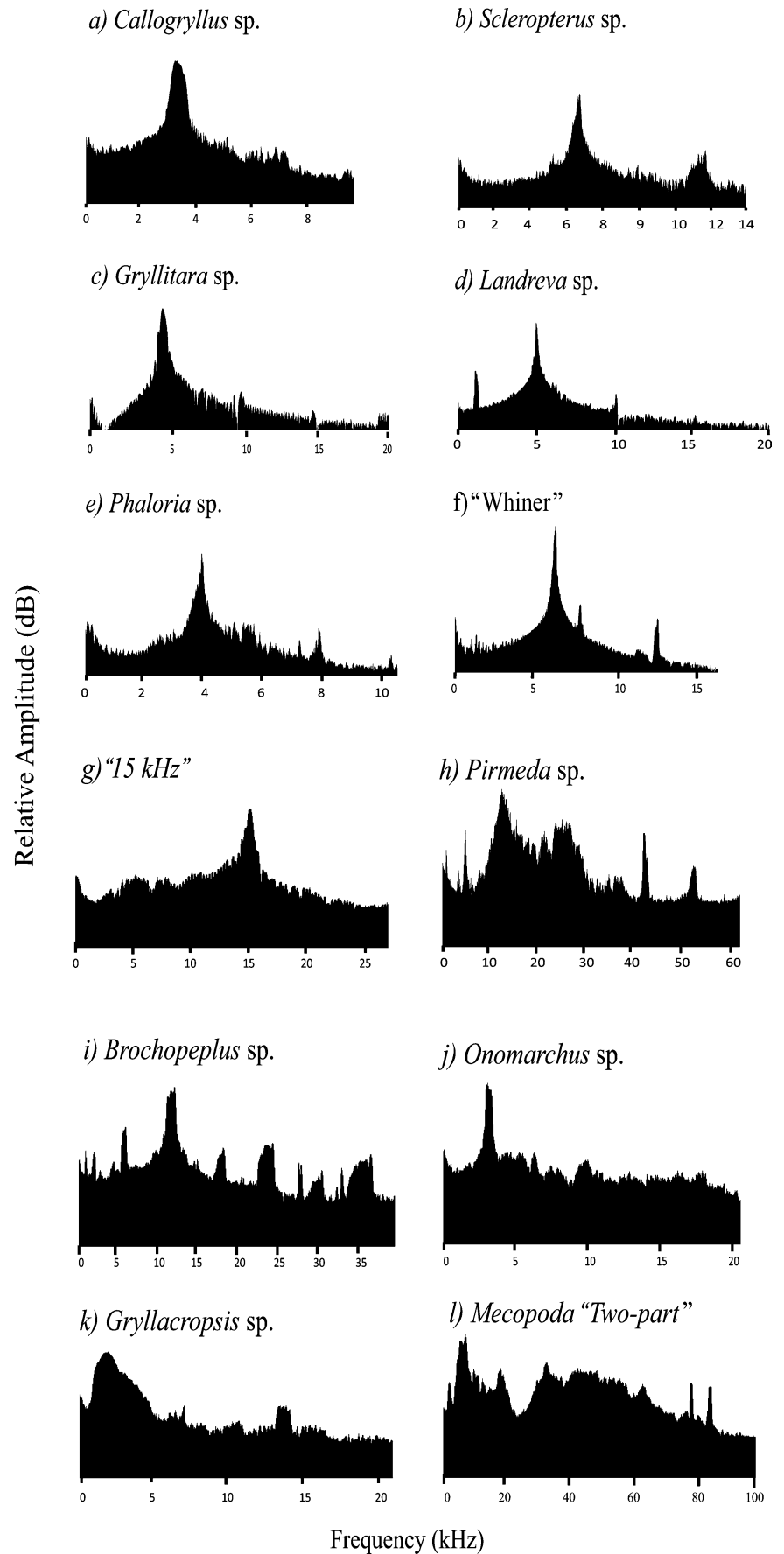


Figure 2
Power spectra of the calls of the 12 ensiferan species tested.

allowed us to approximate the frequency tuning of cricket species (assuming receivers with frequency tuning approximately matched to the calls of their species). At every location, we carried out 4 SPL readings. We also noted the SPL of ambient noise, with and without the one-third octave filter during each transmission event.

Signal analyses

We used 3 different measures of signal degradation: total attenuation, SNR, and overall envelope distortion. The analyses were carried out for the 12 call types for all 5 transmission heights. A species was considered to be adapted to its native singing height if the signal degradation of that species was lowest at that height and was significantly different from that at most other heights.

Attenuation

We used total attenuation rather than excess attenuation because the former is the more biologically relevant measure. Using SPL measurements, we calculated the total attenuation with distance for each of the 12 species as the total drop in SPL with distance. For each call structure–height combination, SPL values were plotted against \log_{10} of distance, and a linear regression was carried out. The rate of attenuation (slope of the regression line) was used for all further analyses. Since the SPL/ SNR/ cross-correlation coefficient always decreased with distance, slope values were always negative. Therefore, for ease of analysis, the modulus of the slope was used in all cases.

SNR

For analyses of SNR and envelope distortion, we ran a custom-written frequency compensation algorithm in MATLAB on all recordings to eliminate the possibility of any bias arising from the instrument's internal frequency response. We calculated the SNR for the recordings using a custom-written signal analysis program in MATLAB (Hastagiri Prakash, CSA, IISc) that utilizes a thresholding technique in order to demarcate signal from noise. The technique involved rectifying the signal by squaring to get at instantaneous power (IP). Using a convolution function, we smoothed the signal and stored the resultant vector. The vector was then sorted in increasing order of the magnitude of IP. The program then searched for a point where the proportional increase in IP is the greatest as compared with the immediately preceding point. The value at that point was used as the threshold, marking the shift from signal to noise. This value is used to classify every point as either signal or noise. After carrying out the thresholding and identifying all signal and noise points, SNR was calculated in dB using the formula:

$$\text{SNR (dB)} = 10 \times \log_{10} \left(\frac{\text{energy in the noise signal} - \text{energy in noise}}{\text{energy in the noise}} \right)$$

For each species, at least 30 chirps (10 per recording) were analyzed at each recording location. The SNR for every recording location was then plotted against distance. Similar to the attenuation data, the x -axis values (distance) were \log_{10} transformed and a linear regression was carried out. The slope of the regression line was used for the statistical analyses.

Envelope distortion

We estimated the distortion of the signal envelope by comparing the envelopes of the reference signal (rerecorded call at 0.5 m) with those recorded after propagation through the habitat at further distances. Five chirps (which were not overlapped by transient noise) were selected from each of the 3 recordings for each call structure–height–distance combination.

Consequently, there were 15 chirps for each species per recording location. The calls were bandpass filtered to remove all non-signal frequencies and the signals rectified. We were interested in dissociating attenuation of signals from temporal distortion to eliminate the possibility of a lower match between signals arising due to severe attenuation. To achieve this, we normalized envelopes of both reference and degraded signals. With such a protocol, what is assessed is the amount of change in the envelope of the signal and not the overall amplitude differences between the 2 signals being compared. We then compared the normalized envelopes of reference and rerecorded signals using a cross-correlation function in MATLAB. The advantage of this routine is that the signals need not be aligned for comparison because the routine slides the 2 signals against each other. The value of the cross-correlation coefficient is highest when the maximum match is achieved. We used the cross correlation coefficients to signify the degree of distortion of the signal envelope. We plotted the cross-correlation coefficient values for every recording location against \log_{10} -transformed distance and we fit a linear regression to the curve. We obtained the slope (rate of decay) from the regression equation and carried out further statistical analyses on the slope values.

Statistical analyses

The AAH predicts least degradation in native habitats (here, heights). Therefore, for the AAH to be upheld, the drop in SPL, SNR, and/or cross correlation coefficients with distance should be least when calls are broadcast at the native height. This means that the slope values for each of the 3 measures of degradation should be lowest for a species at its native height and statistically significantly different from the corresponding slopes at all or most other heights. To test this, for each of the 3 measures of degradation, we log transformed the slope values to attain normality. Where normality was achieved, we subsequently carried out 2-way factorial analyses of variance (ANOVAs) (attenuation and SNR data), which were examined for the independent effects of height and signal structure on call propagation. We also examined the interaction effects between height and call type to test if certain species do better at certain heights. Because the data from envelope distortion did not follow a normal distribution even after log transformation (Kolmogorov–Smirnov $P < 0.01$), we instead carried out a Kruskal–Wallis (nonparametric) test to examine the effect of height and call structure. Due to the limitation of a nonparametric test, however, testing for an interaction was not possible. If significant results were obtained (significance level, $\alpha = 0.05$), we carried out further analyses on the corresponding data set as follows:

- 1) We ranked the mean slope values for the 5 heights.
- 2) We identified and assigned the height with the lowest slope value (least decay) as the best height for transmission (contingent on statistical significance).
- 3) We then examined if this height was the native height for that species.
- 4) We compared the mean slope value at the height of least degradation with that of the next best height to examine if they were significantly different using t -tests (attenuation and SNR data; $\alpha = 0.05$) or Mann–Whitney U tests (envelope distortion data; $\alpha = 0.05$).

RESULTS

Microclimatic conditions and background noise level

The day temperatures (median value = 23.6 °C, 9–11 AM) were not significantly different from the calling time (6–9 PM) temperatures (median value = 23.6 °C; $U = 9$; $P = 0.732$;

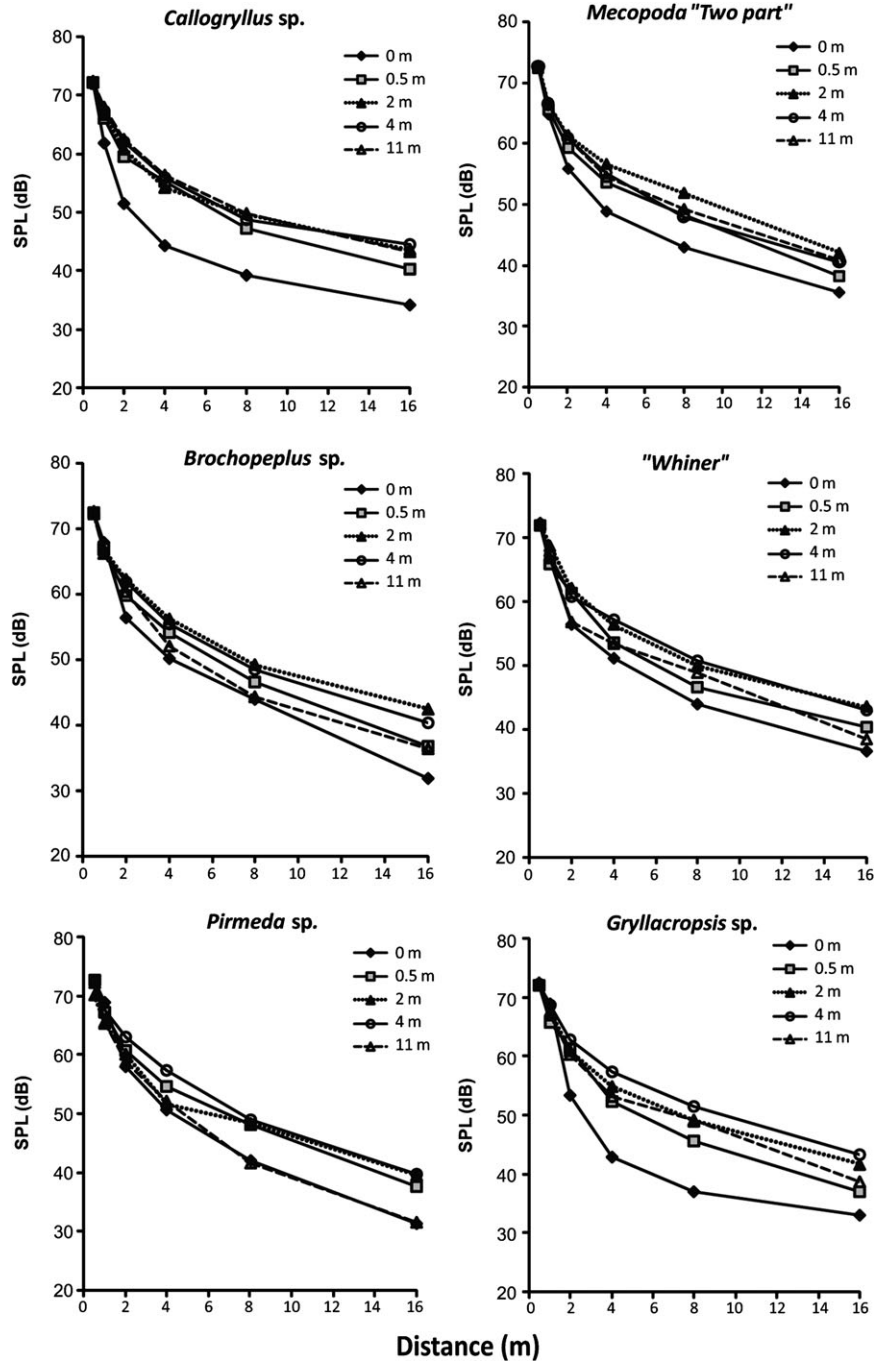


Figure 3
Attenuation profiles of 6 of 12 species tested. The species have been selected to represent the taxonomic breadth, range of native calling heights, and diversity in temporal and spectral features of calls. *Brochopeplus* sp., "Whiner", and *Pirmeda* sp. upheld the AAH, whereas *Callogryllus* sp., *Mecopoda* "Two-part", and *Gryllacropsis* sp. refuted the predictions of the AAH with respect to signal attenuation.

Supplementary Figure S1a). The median slope value of the regression curves fitted to the temperature data (to measure temperature gradient with height) was around 0 for day temperatures and around -0.1 for night temperature readings (Supplementary Figure S1b). The average difference between the temperatures measured at the ground and at 8 m for daytime measurements was 0.8 °C (standard error [SE] ± 0.11 , $N = 36$) and for the night was 1.25 °C (SE ± 0.12 , $N = 36$), indicating the absence of strong temperature gradients between the ground and lower canopy (Supplementary Figure S2). We therefore selected the time period between 9 and 11 AM for the transmission experiments. Across all time periods, relative humidity was approximately

90–100%, and there was no wind inside the forest up to the maximum measured height of 8 m.

Overall, background noise levels were lower in the canopy as compared with the understorey for all filter settings. The average background noise for the centre frequencies 1.6, 3.2, 5, 6.3, and 16 kHz varied between 14.5 and 28.2 dB SPL ($N = 10$ at each height; ref: 2×10^{-5} N/m²). Average background noise for the 500 Hz high-pass filtered measurements was 28.3 dB SPL (± 0.8 standard deviation [SD], $N = 10$) in the canopy and 35.5 dB SPL (± 1.27 SD, $N = 10$) in the understorey. This formed the noise floor of the forest when transient sounds were not present.

Table 2
Results of 2-way factorial ANOVAs testing the effect of height and species-specific call structure on signal attenuation and SNR

	Sum of squares	df	Mean squares	F	P value
A) Attenuation					
Height	0.2410	4	0.0603	648	<< 0.001*
Species	0.1439	11	0.0131	141	<< 0.001*
Height × Species	0.0994	44	0.0023	24	<< 0.001*
Error	0.0167	180	0.0001		
B) SNR					
Height	0.54	4	0.14	148.55	<< 0.001*
Species	0.78	11	0.07	77.33	<< 0.001*
Height × Species	0.95	44	0.02	23.62	<< 0.001*
Error	0.11	120	0.00		

Acoustic adaptation with respect to vertical stratification of calling heights

Attenuation

The attenuation profiles of 6 of 12 species tested in this study are shown in Figure 3. A 2-way factorial ANOVA revealed an independent effect of height (Table 2), indicating that calls attenuate differently at different heights independent of the differences in their call structure. There was also an independent effect of call type, indicating that certain call types attenuate more than others, independent of the height of transmission. There was a significant interaction between height and call type, signifying that certain species perform better at certain heights.

Pairwise comparisons of ranked mean slope values revealed that, for 5 of 12 species tested, the native height of calling was the best or one of the best heights for signal propagation (Table 3). These 5 species (“Whiner”, *Phaloria* sp., “15 kHz”, *Brochopeplus* sp., and *Pirmeda* sp.), though very different in their call features, were all understorey species calling from either the mid or the upper understorey (Table 1).

SNR

SNR profiles with distance of 6 of 12 species tested are shown in Figure 4. As in the case of attenuation data, a 2-way factorial ANOVA revealed an independent effect of height and call type. There was also a significant interaction between height and call type (Table 2). Pairwise comparisons showed that

only 3 of 12 species had best transmission at their native heights with respect to SNR (Figure 7; Table 3). These 3 species call from 3 different layers and have very different call features. Whereas the high frequency broadband caller *Mecopoda* “Two-part” sp. calls from close to the ground in the lower understorey (0.5 m), *Gryllacropsis* sp. calls from high up in the canopy (11 m) and has a low frequency (1.7 kHz), relatively narrow bandwidth call (Table 1). *Brochopeplus* sp. on the other hand is a narrow bandwidth, high frequency (dominant frequency = 11.6 kHz) caller that calls from the mid understorey (2 m), and was the only species that overlapped with the 5 species that upheld the prediction of the AAH with respect to attenuation (Figure 7).

Envelope distortion

There was a strong independent effect of calling height (degrees of freedom [df] = 4, N = 900, H = 357.02; P < 0.001) and of call type (df = 11, N = 900, H = 155.37; P < 0.001) on the degree of distortion (for some examples of height-dependent envelope distortion, see Figures 5 and 6). Here again, only 3 of 12 species showed best transmission at their native heights (Figure 7; Table 3). The 3 species were *Gryllacropsis* sp. and *Brochopeplus* sp. (which also showed acoustic adaptation with respect to SNR) and an upper understorey (4 m) caller, “Whiner” (Podoscirtinae).

Height-dependent effects

Signal degradation was worst along the ground with respect to all 3 measures irrespective of signal structure (Table 3). At least 10 of 12 species suffered most degradation along the ground. The mid and upper understorey (2 and 4 m) were the best heights for transmission with respect to attenuation and envelope distortion (Table 3).

DISCUSSION

We have provided for the first time a test of the AAH at the microhabitat level with respect to vertical stratification of an assemblage of 12 coexisting species of crickets and katydids in a tropical rainforest. The results do not provide overall support for the hypothesis that vertical stratification of calling sites is driven by acoustic adaptation. Different sets of species supported the hypothesis depending on which attribute of signal degradation was examined. Finally, we found strong height-dependent influences on signal degradation independent of signal structure, with the ground emerging as the worst and the understorey as the best layer for signal propagation.

Table 3
Best and worst calling heights for 12 species of Ensifera tested with respect to 3 measures of signal degradation

Species	Native height (m)	Attenuation		SNR		Envelope distortion	
		Best height (m)	Worst height (m)	Best height (m)	Worst height (m)	Best height (m)	Worst height (m)
<i>Mecopoda</i> “Two-Part”	0.5	2, 11	0	0.5, 2	0, 11	2	0
<i>Callogryllus</i> sp.	0	2	0	0.5, 2	0	4	0
<i>Scleropterus</i> sp.	0	4	0	0.5, 2	4, 11	2, 11	0
<i>Gryllitara</i> sp.	0	11	0	—	0	4, 11	0
<i>Gryllacropsis</i> sp.	11	4	0	11	0	11	0
<i>Landreva</i> sp.	0.5	11	0	—	0, 0.5	4	0
“Whiner”	4	4	0	11	0, 0.5	4, 11	0
<i>Phaloria</i> sp.	2	2	0	—	—	4	0, 0.5
“15 kHz”	4	2, 4	11	0.5	0, 4	0.5	0
<i>Brochopeplus</i> sp.	2	2	0	2	0	2	0
<i>Pirmeda</i> sp.	4	2, 4	0, 11	0.5	0, 4	2	0
<i>Onomarchus</i> sp.	11	2, 4	0	2	0, 0.5	4	0

Bold indicates that the native calling height was the best or one of the best heights for transmission. —, no clear best/worst height.

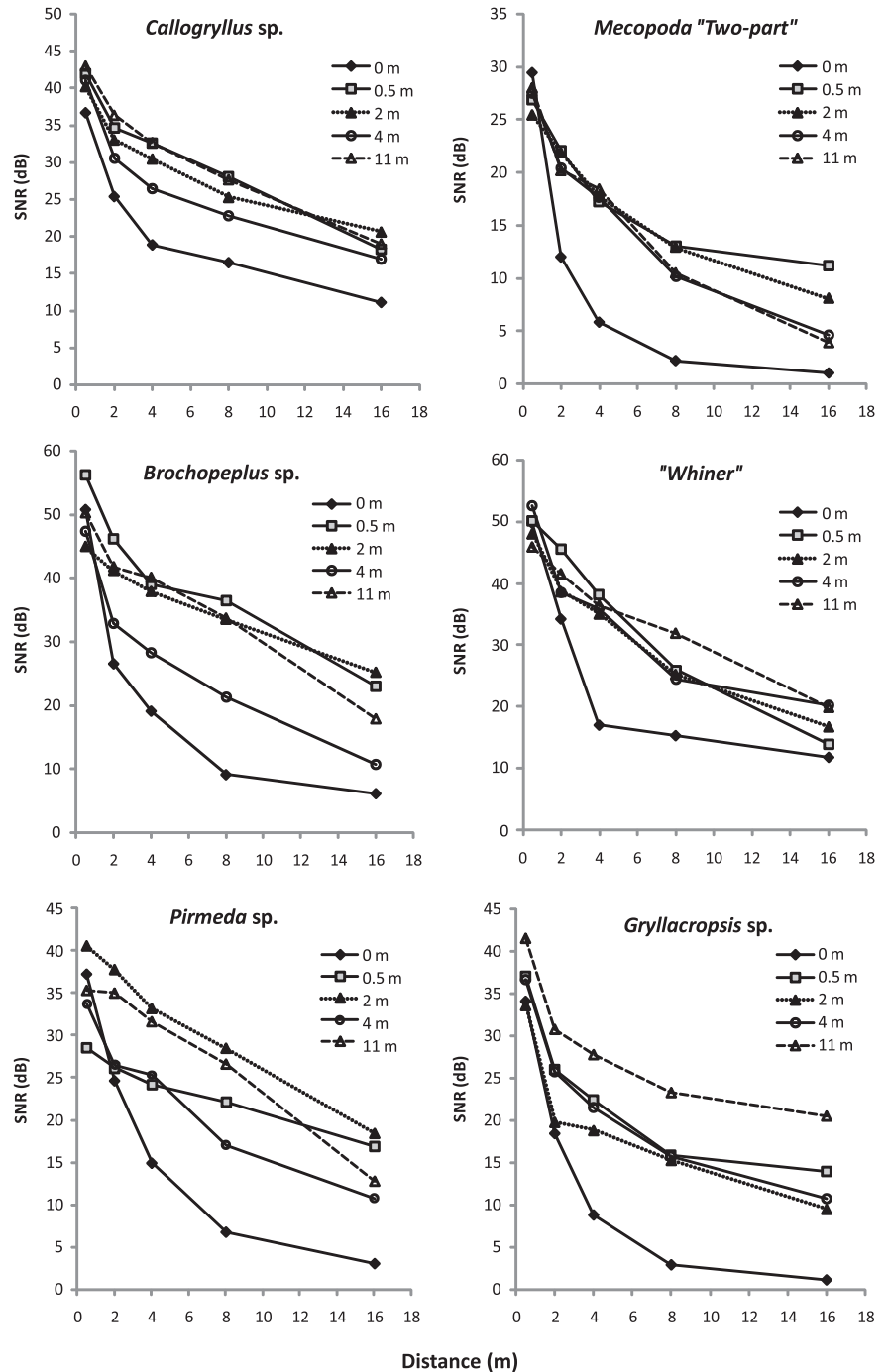


Figure 4
SNR profiles of 6 of 12 species tested. The species have been selected to represent the taxonomic breadth, range of native calling heights, and diversity in temporal and spectral features of calls. *Brochopeplus* sp., *Mecopoda* "Two-part", and *Gryllacropsis* sp. upheld the AAH, whereas *Callogryllus* sp., "Whiner", and *Pirmeda* sp. refuted the predictions of the AAH with respect to SNR.

AAH: previous tests

Studies supporting the AAH have either demonstrated greater signal transmission efficiency in native habitats or shown the use of habitat-dependent song features by species as predicted by the AAH. Most support for the AAH comes from studies on avifauna (Morton 1975; Wiley and Richards 1982; Cosens and Falls 1984; Ryan and Brenowitz 1985; Tubaro and Segura 1994; Tobias et al. 2010) and primates (Waser and Brown 1986; Brown et al. 1995). Even in birds, however, several studies have shown mixed (Date and Lemon 1993; Nemeth et al. 2001; Blumstein and Turner 2005) or no support for the AAH (Lemon et al. 1981; Tubaro and Mahler 1998). In the case of frogs, the AAH has little support from empirical studies (Penna and Solis 1998; Kime et al. 2000).

In acoustically communicating insects, only 2 studies have examined signal transmission in the context of adaptation to calling microhabitat/habitat (Sueur and Aubin 2003; Couldridge and van Staaden 2004). One study was carried out on 7 species of grasshoppers that were native to forests, savanna, fynbos, and karoo macrohabitats in South Africa (Couldridge and van Staaden 2004). In this study, the prediction of the AAH was tested by carrying out playback experiments in all 4 vegetation types. The results provided support for the AAH by demonstrating lower levels of distortion of calls in native habitats as compared with non-native habitats. The other study was carried out on 2 cicada species (Sueur and Aubin 2003) at 2 heights (0.3 and 1.3 m) within a vineyard. In this study, calling site selection was not found to be related to constraints on signal

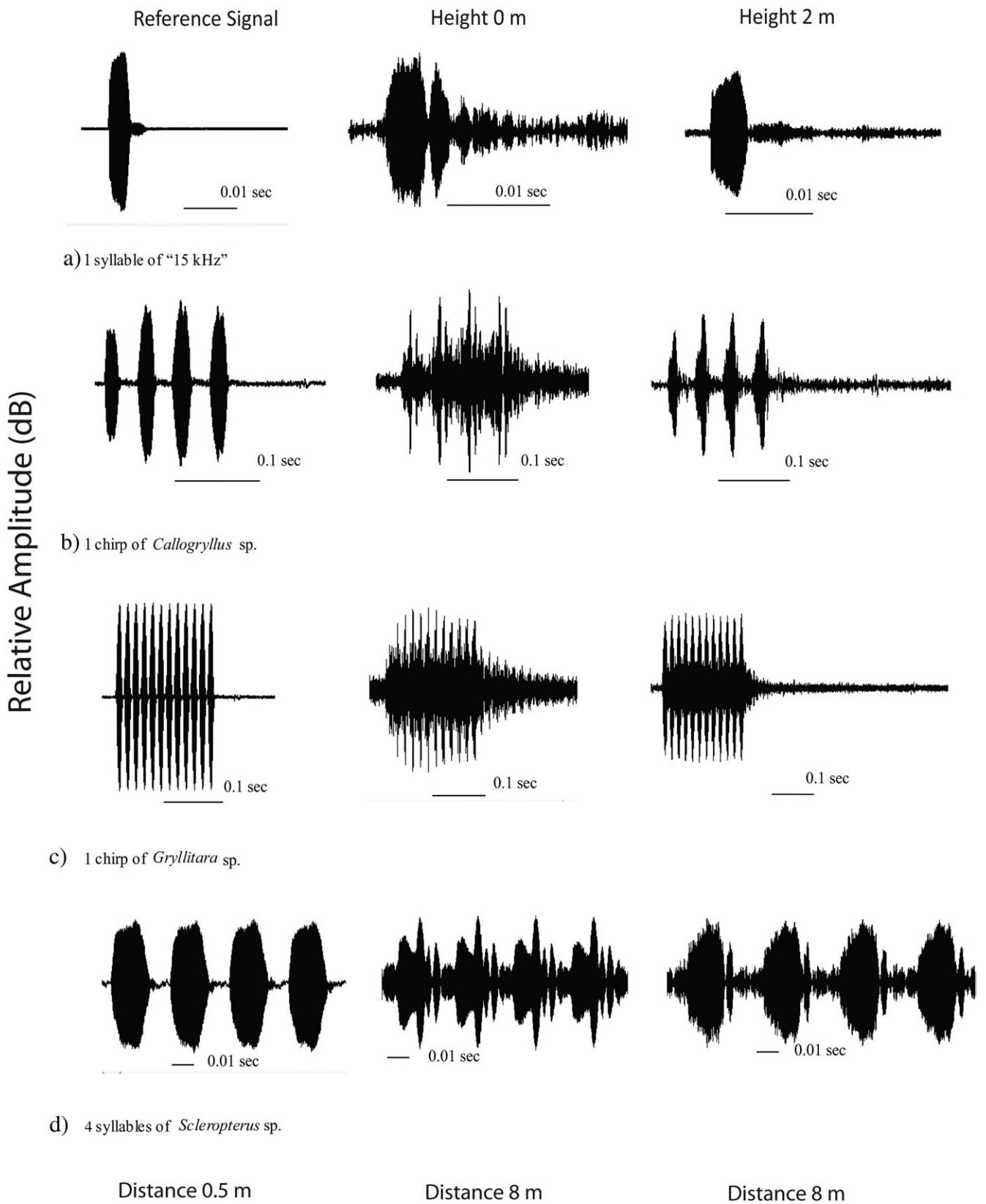


Figure 5 Oscillograms of some exemplars of calls rerecorded at 0.5 and 8 m distance from the speaker to illustrate call distortion at 2 heights (0 and 2 m).

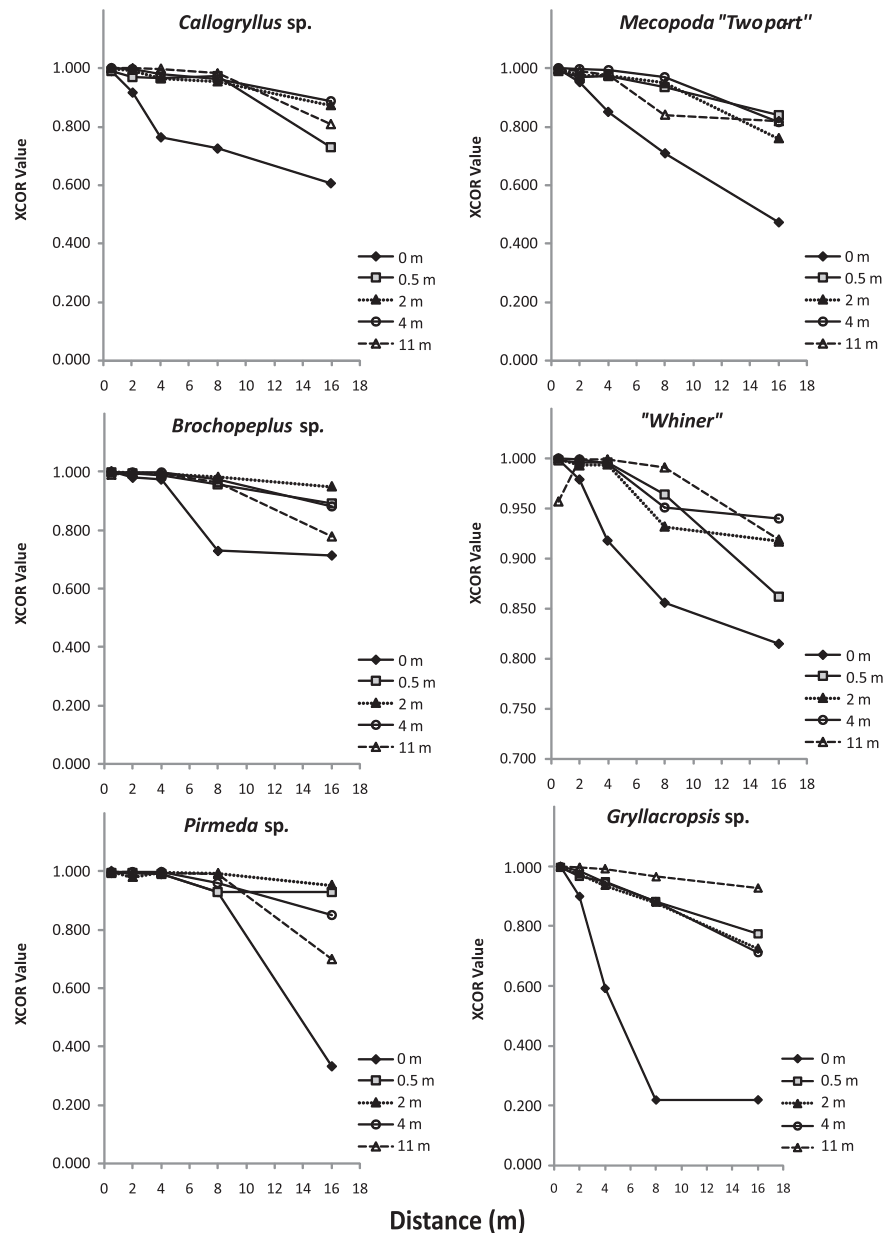


Figure 6

Decrease in the cross-correlation coefficients with distance at different heights. The species have been selected to represent the taxonomic breadth, range of native calling heights, and diversity in temporal and spectral features of calls. *Brochopeplus sp.*, "Whiner", and *Gryllacropsis sp.* upheld the AAH, whereas *Callogryllus sp.*, *Mecopoda "Two-part"*, and *Pirmeda sp.* refuted the predictions of the AAH with respect to envelope distortion.

propagation. This study is the only previous investigation of the AAH at the microhabitat level.

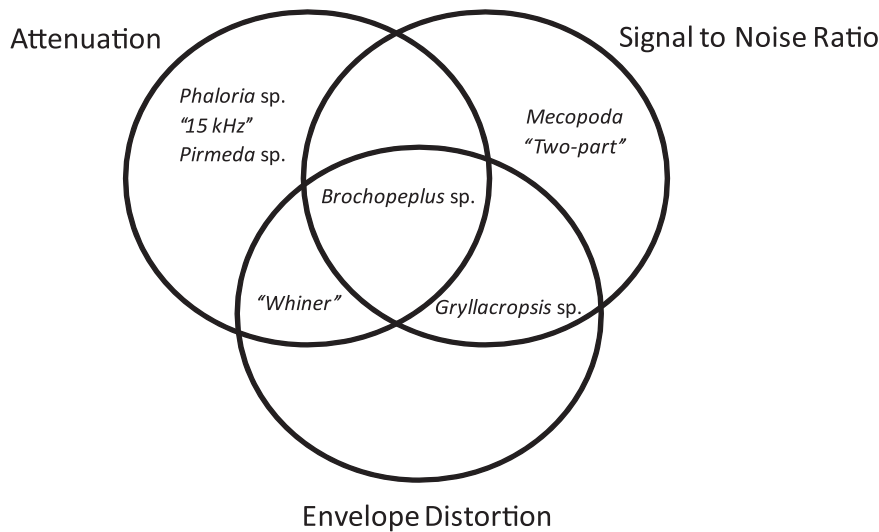
Acoustic adaptation in relation to vertical stratification of calling heights

The importance of transmission height has been demonstrated widely in vertebrate taxa, and it has been shown that degradation decreases with speaker height (Marten and Marler 1977; Mathévon et al. 1996, 2005; Kime et al. 2000; Nemeth et al. 2001). Height-dependent transmission has also been examined in insects such as bladder grasshoppers (Couldridge and van Staaden 2004), cicadas (Sueur and Aubin 2003), and different bushcricket species of temperate regions (Keuper et al. 1986; Arak and Eiriksson 1992; Römer and Lewald 1992). Signal attenuation was found to decrease with sender height in most cases. Nemeth et al. (2001) tested the AAH with respect to calling heights in 5 coexisting species of antbirds. They found a significant effect of transmission height on signal degradation, with 3 of 5 species showing optimal transmission at species-specific heights.

In our study, we did not find overall support for the AAH as a driver of vertical stratification in this cricket assemblage. Of 12 species examined, only 3 supported the AAH with respect to 2 measures of degradation, whereas only 1 species (*Brochopeplus sp.*) supported the hypothesis from all measures of degradation. In fact, 5 of the 20 species in this assemblage call exclusively from the ground (Diwakar and Balakrishnan 2007b), which is the worst layer for propagation with respect to all aspects of signal degradation. It is therefore unlikely that habitat acoustics constitutes a major selection pressure driving vertical stratification of calling heights and the explanation for selection of singing heights in these cricket species needs to be sought in other evolutionary forces such as predation pressure and masking interference.

Test of acoustic adaptation with different measures of degradation

The observation that different sets of species upheld the hypothesis depending on the measure of degradation examined

**Figure 7**

Venn diagram showing overall results of the test of the AAH by 3 measures of signal degradation. The species listed are the ones whose degradation profiles upheld the AAH.

may be explained by the fact that different species may be trying to maximize different aspects of signal transmission. From the point of view of a sender, some may maximize broadcast area, whereas others may maximize signal structure preservation. For a receiver, however, higher energy in the signal is not sufficient for signal detection if the SNR for such signals is low due to higher ambient noise. Therefore, from the point of view of biologically meaningful signal detection in this assemblage, only 3 species are in optimal calling positions (Figure 7). With respect to signal temporal structure preservation also, only 3 species occupied optimal calling positions.

In conclusion, the lack of support for the AAH may point to a problem with an inherent assumption that animals are trying to maximize transmission range. Species may instead be trying to transmit signals over an optimal range or relevant distances (Lemon et al. 1981; Brown and Handford 2000; Naguib and Wiley 2001; Nemeth et al. 2006). For instance, if the intended receivers (neighbors or mates) are nearby, or if a certain amount of degradation in a signal is permissible, the need for maximizing transmission may not arise (Aubin et al. 2004, Kroon and Westcott 2006).

Competition for acoustic space could be another factor influencing the choice of calling sites. If the best heights for signal transmission have already been occupied by some species, then other species may be driven to occupy less optimal positions for calling. Under strong acoustic competition for broadcast space in areas of high species diversity, avoidance of masking interference could influence the choice of singing sites. Therefore, it would be interesting to examine if less diverse communities better uphold the predictions of the AAH with regard to vertical stratification of calling sites.

Moreover, the signals may also attract predators and parasites (Endler 1993), and this may impose a selection pressure against maximizing transmission. Comparison of sites with high and low predator densities could be carried out to examine the effect of predation pressure in determining choice of singing sites and the adherence to the predictions of the AAH.

The choice of singing sites and therefore vertical stratification is likely to be a trade-off between increasing broadcast space, avoiding masking interference, and being less conspicuous to eavesdropping predators.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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