Habitat-dependent transmission of male advertisement calls in bladder grasshoppers (Orthoptera; Pneumoridae)

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Summary

It has been hypothesized that the physical properties of the environment exert selection pressure on long-range acoustic communication signals to match the local habitat by promoting signal characteristics that minimize excess attenuation and distortion. We tested this in a unique family of bladder grasshoppers notable for producing a signal with a 2 km maximum transmission distance. In direct performance comparisons, male advertisement calls of seven species were broadcast through four vegetation biomes – forest, fynbos, savanna and succulent karoo. The calls of species native to forest and fynbos biomes propagated with lower levels of distortion over distance in their respective habitats relative to those of non-native species, while fynbos species also performed best in the remaining two habitats. In addition, both forest and fynbos species had low levels of signal attenuation over distance in all environments. The fynbos biome was characterized by high inconsistency in signal degradation, while the forest biome had the highest levels of environmental noise. Innate habitat characteristics, leading to comparatively limited acoustic communication distances in the forest and fynbos relative to the savanna and succulent karoo, may therefore explain the need for a higher quality of signal transmission in grasshoppers inhabiting the former two environments.

Key words: acoustic communication, advertisement call, habitat, bladder grasshopper, Pneumoridae, sound transmission, spectrographic cross correlation.

Introduction

Acoustic signals are commonly utilized for communication over long distances by a variety of animal taxa, from butterflies (Yack et al., 2000) to elephants (McComb et al., 2003). However, one of the major predicaments plaguing long-range signallers is that sounds become progressively more degraded the further they propagate. The transmission of acoustic signals through any given environment results in modification of the signal amplitude and fidelity over distance. Loss of amplitude, resulting from spherical spreading and also from absorption and scattering of sound waves (excess attenuation), diminishes the range at which receivers can detect a signal, while loss of fidelity, incorporating frequency-dependent attenuation, irregular amplitude fluctuations and reverberations, reduces the ability of receivers to accurately recognize a signal in the event it is detected. A combination of changes in both amplitude and fidelity contributes to overall patterns of signal degradation.

The rate of acoustic signal degradation, and subsequently the range at which sounds can be used effectively for communication purposes, is dependent upon numerous factors. These include spectral and temporal properties of the signal itself (Wiley and Richards, 1978), behavioural modifications of the animal during signalling, such as calling from preferential heights and locations (Bennet-Clark, 1987; Keuper

et al., 1986), and external properties of the local environment, incorporating vegetation type (Lang, 2000), meteorological conditions (Garstang et al., 1995), and acoustic interference from other organisms (Wollerman, 1999).

The acoustic adaptation hypothesis emanated largely from the work of Morton (1975) and Hansen (1979) and was conceived as a means of means of investigating the relationship between animal vocalizations and ecological factors. This hypothesis was based on the observation that environmental factors may heavily influence the evolution of long-range acoustic signals by imposing selection pressures that act to modify the sound properties of signals in order to maximize their broadcast range and the number of potential receivers (Endler, 1992; Forrest, 1994; Morton, 1975). This could lead to a matching between signal and environment, such that signals transmit optimally in native habitats and, conversely, perform poorly when broadcast through non-native habitats.

Studies concerning the propagation of long-range acoustic signals in relation to the environment in which they are transmitted have yielded mixed results. The acoustic adaptation hypothesis for enhanced transmission efficiency in native habitats has garnered support primarily from studies on avian and primate taxa. Birds inhabiting different

environments produce vocalizations with characteristics suited to enhancing transmission in their native habitats (e.g. Bertelli and Tubaro, 2002; Bowman, 1979; Cosens and Falls, 1984; Gish and Morton, 1981; Handford, 1981; Morton, 1975; Wiley, 1991). Moreover, calls broadcast in different environments exhibit differential rates of excess attenuation and/or distortion in both birds (e.g. Dabelsteen et al., 1993; Shy and Morton, 1986) and primates (e.g. Brown et al., 1995; Waser and Brown, 1986; Waser and Waser, 1977). In contrast, the influence of the environment on the evolution of signal characteristics has been more difficult to establish in anurans. Most studies have failed to find a significant correlation between habitat acoustics and either signal characteristics (Zimmerman, 1983) or signal propagation (Castellano et al., 2003; Kime et al., 2000; Penna and Solís, 1998; but see Ryan et al., 1990). Variability in detecting the effects of habitat selection are likely to be due to the multiplicity of additional factors that affect the evolution of signals. Mismatches between signal and environment, which would potentially mask the effects of habitat selection, could arise from predator avoidance, competition avoidance, sexual selection, phylogenetic history, and variation in the relative strengths of competing selection pressures. Here we test the acoustic adaptation hypothesis for bladder grasshoppers (Orthoptera, Pneumoridae) through an examination of acoustic signal transmission of species-specific male mating calls in different habitat types. This is the first detailed examination of the relationship between the environment and sound propagation in an invertebrate group specialized for long-distance signalling. We focus exclusively on habitat effects, since constraints imposed by acoustic characteristics of the habitat provide the framework within which other selection pressures must operate. We thus anticipate an effect that is detectable, though perhaps not strong.

Bladder grasshoppers comprise a small family of up to 17 species (Dirsh, 1965), with behaviour and morphology uniquely suited for pair-formation *via* acoustic duetting over distances of at least 50 m (van Staaden and Römer, 1997). With the aid of an air-filled, inflated abdomen functioning as an acoustic resonator, males produce a nocturnal advertisement call that is both extremely loud (98 dB SPL at 1 m) and relatively low in frequency (1.4–3.2 kHz) for an insect only 50 mm in length. Together with six pairs of highly sensitive abdominal hearing organs (van Staaden and Römer, 1998), this enables male signals to attain a viable transmission distance of up to 1.9 km at night (van Staaden and Römer, 1997). Male signalling functions as the primary basis for pair formation, with non-flighted receptive females producing a softer response, enabling flighted males to locate them. The male advertisement calls of pneumorids possess a high degree of species specificity, displaying substantial variation in both temporal and structural properties among species. However, despite these broad interspecific differences in the male signal, courtship and mating follow a stereotyped sequence in all species, and female calls are virtually indistinguishable. Here we focus our attention on male signals, due to both the lack of

discernable differences in the female signal and the shorter transmission distances thereof.

Pneumorids are endemic to the coastal regions of southern Africa, where they are found in four distinct vegetation biomes: forest, savanna, fynbos ('fine bush') and succulent karoo (Rutherford, 1997). These four habitat types represent a wide range of environmental conditions, varying in extremes from dense, humid, forested areas to open, arid, semi-desert areas. The forest biome is confined mostly to the wetter eastern seaboard, where it is extremely patchy in distribution and comprises a very small total land area. Forest vegetation at the site of transmission experiments comprised a closed canopy of woody vegetation up to 25 m tall and was dominated by *Leucosidea sericea* and *Ficus thonningi,* with trunk diameters reaching 1 m, and an understory of *Maytenus acuminata*, *Hypericum* and *Helichrysum* spp. The subtropical savanna biome, by far the largest biome in southern Africa, consists of grasses interspersed with taller woody vegetation. The area where experiments were conducted fell under the class of broad-leaved savanna. This is a typical C4 grassland with *Themeda*, *Tristachya*, *Trachypogon* and *Aristida* spp. being the most prominent components, and average grass height reaching approximately 0.5 m. The fynbos biome occupies the most southern and south-western regions of southern Africa and is characterized by evergreen, fine-leaved shrubs of intermediate height. Fynbos vegetation is renowned for its unparalleled species diversity and is characterized by the presence of three distinctive elements *viz*. restioids and ericoid shrubs, both ranging in height from 0.5 m to 2 m, and overstory proteoid shrubs reaching a maximum height of 5 m (Cowling et al., 1997). The sparsely vegetated succulent karoo biome derives its name from the low-lying leaf-succulent plants that dominate this biome. It is located along the western coast of southern Africa and represents an intermediate state between the less arid fynbos to the south and true desert to the north. Succulent karoo vegetation, although similar to fynbos in some respects, has a relatively higher proportion of bulbous plants, and the vegetation is lower growing, sparser, and comprises more succulents than fynbos.

Our primary objective was to evaluate the relative importance of the environment in shaping signal evolution by comparing signal degradation across the four habitat types for seven species of bladder grasshopper. Of these, one species (*Pneumora inanis* Fabricius) was classified as being native to the forest, three (*Bullacris intermedia* Péringuey, *B. membracioides* Walker, *B. serrata* Thunberg) native to the savanna, two (*B. obliqua* Thunberg, *Physemacris variolosus* L.) native to the fynbos, and one (*B. unicolor* L.) native to the succulent karoo. With one exception, all species have geographic ranges that fall exclusively into one biome. However, *B. unicolor*, which is predominantly a succulent karoo species, extends slightly into the fynbos along the edges of its geographic distribution. In concordance with the acoustic adaptation hypothesis, we test the prediction that the transmission efficiency of long-distance signals is greater in native habitats relative to that in non-native habitats,

specifically with respect to (i) transmission distance and (ii) signal fidelity.

Materials and methods
Field sites

Field experiments were conducted between 20:00 h and 24:00 h during January and October 2002, coinciding with both the active time-period and the seasonal occurrence of the animals. Four locations in South Africa with undisturbed vegetation, each falling within one of the biomes of interest, were selected as field sites for the transmission experiments (Fig. 1). These were: (1) Goegap Nature Reserve in Springbok, Northern Cape province: succulent karoo biome; (2) Wolfkop Private Nature Reserve in Citrusdal, Western Cape province: fynbos biome; (3) Krantzkloof Nature Reserve in Kloof, KwaZulu-Natal province: savanna biome; and (4) a private farm at Bulwer, KwaZulu-Natal province: forest biome. Mean relative humidity and temperature measures for the field sites were estimated at 58% and 18°C in the succulent karoo, 63% and 16°C in the fynbos, 87% and 21°C in the savanna and 69% and 19°C in the forest.

Test sounds

Sound recordings of male advertisement calls used in the transmission experiments (i.e. test sounds) were exemplars selected from a previously recorded sound library. These songs were recorded in the laboratory using a sound level meter (Bruel & Kjaer, model 2009; Naerum, Denmark) and a microphone (1/2″ condenser, type 2540, Larson & Davis, Provo, UT, USA; A weighting, RMS fast) placed 1 m dorsal to a calling male in a wire mesh cage. Songs were sampled at 44.1 kHz on an Apple Macintosh Powerbook *via* the built-in 16-bit A/D soundboard and subsequently edited with SoundEdit™16 (San Francisco, CA, USA). Male call characteristics, including length, frequency and temporal patterning, vary substantially among species (Table 1, Fig. 2). Background noise was generally low in the laboratory setting, thus test sounds had equivalent low levels of background noise for each species. For each species, a single exemplar was selected, based on average call characteristics for the species. For ease of comparison, all calls were amplified to a uniform peak amplitude value (amplification range: 0.8–19.1 dB). The order of signal presentation was randomized and inter-song
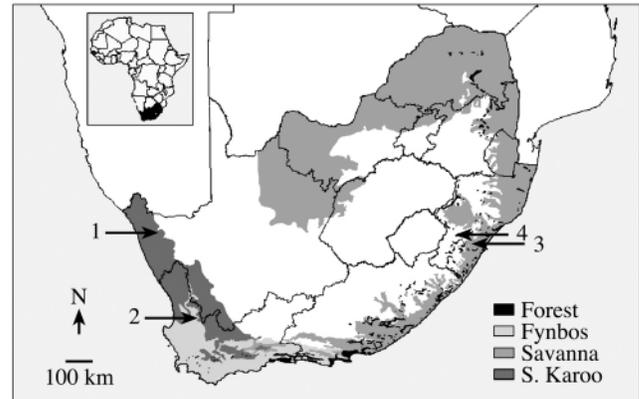

Fig. 1. Map of South Africa showing the four biomes of interest and the locations of the field sites where the transmission experiments were conducted: 1, Springbok; 2, Citrusdal; 3, Kloof; 4, Bulwer. Lines within South Africa indicate provincial boundaries.

pauses of 3 s for repetitions of the same call and 5 s for different calls minimized the risk of forward-masking. In other words, this time window was sufficient to prevent reverberations of the previous call overlapping with the next signal.

Transmission experiments

Experiments were carried out in which advertisement signals of seven pneumorid species were broadcast and re-recorded along a transect at various distances and heights from the sound source. An identical protocol was followed in each of four habitat biomes. All sound transmission experiments were conducted when wind speed was less than 1 m s^{-1} and ambient noise levels relatively low. A single speaker elevation (1.5 m) and three microphone heights (0.2 m, 1 m, 2 m) were selected as representative caller heights and receiver locations, respectively. Signal propagation was assessed for three different receiver elevations, since female restriction to their specific host plants determines the most likely transmission channel. Males of most bladder grasshopper species call at the intermediate height of 1.5 m (M. J. van Staaden, personal observation), corresponding with the maximum vegetation height in most habitats. The only notable exception is the forest-dwelling *P. inanis*, which has a propensity to call at

Table 1. *Physical characteristics of the male bladder grasshopper advertisement calls used in the study*

Species	Peak frequency (kHz)	Call length (s)	Final syllable length (s)	Number of short syllables	Final syllable repeated
B. intermedia (Savanna)	1.81	2.87	1.10	6	No
B. membracioides (Savanna)	1.72	2.55	0.77	5	No
B. serrata (Savanna)	2.15	1.44	1.13	2	No
B. unicolor (Succulent karoo)	2.07	2.34	1.12	2	No
B. obliqua (Fynbos)	1.55	5.83	4.16	4	No
Ph. variolosus (Fynbos)	3.19	0.66	0.30	2	No
Pn. inanis (Forest)	1.46	9.93	0.28	6	Yes, 10×

higher elevations. Test sounds were broadcast from an Apple G4 laptop computer running SoundEdit™16, and passed through a Pioneer GM-X252 amplifier connected to a Jensen 6944 loudspeaker at the origin of the transect. The broadcast signal was adjusted to a maximum intensity level of 95 dB SPL (re 20 μPa) at a distance of 1 m, as measured with a Larson-Davis DSP83 sound level meter. This value was selected based on the known value for *B. membracioides*, the only species for which natural sound intensity levels have been reliably recorded. While the values for *B. membracioides* are believed to be similar to the natural calling intensity levels of the other species, the possibility exists that some species may call at intensities either higher or lower than the chosen broadcast intensity. Within *B. membracioides*, males always call at the maximal recorded intensity level to advertise their presence, and only reduce the amplitude of their calls when in close proximity to a responding female.

In each of the four field sites, a 100 m straight line transect was marked out along a flat stretch of land bearing representative vegetation. This distance corresponds to the maximum transmission distance at the behavioural response threshold of female *B. membracioides* (van Staaden and Römer, 1997, 1998). The broadcast sounds were re-recorded along the transect at six distances (1 m, 5 m, 10 m, 25 m, 50 m, 100 m) from the sound source using a Marantz PMD 430 (Setagaya, Japan) audio cassette recorder connected *via* a 6 m cable to a wind-shielded, unidirectional microphone (Sennheiser MZW 66; Wedemark, Germany). The horizontally

positioned microphone was shock mounted (Audio-Technica AT 8415, Tokyo, Japan) on a 2 m extendible rod, and aligned with the loudspeaker by eye. Recordings at a distance of 1 m were taken at a height of 1.5 m only, level with the speaker. Under these circumstances, the sounds had suffered negligible habitat-induced degradation, and served both as a control for any sound distortion caused by the recording system and as calibration signals with which to compare recordings taken at greater distances. Six repetitions of each call were recorded at each distance and height over two consecutive nights, in order to better represent the natural variability present under field conditions.

Data analysis

All control (recorded at a distance of 1 m) and observation (recorded at distances greater than 1 m) sounds were digitized onto an Apple MacIntosh G4 computer *via* the built-in sound-board (44.1 kHz sampling rate; 16 bit sample size) and filtered with Canary 1.2 (*Canary: the Cornell Bioacoustics Workstation, Version 1.2*. Cornell Laboratory of Ornithology, Ithaca, NY, USA; 1995) to remove frequencies below 500 Hz and above 12 kHz. This filtering did not compromise any components of the test signal itself. Through auditory and sonogram inspection, we selected as a control sound one of the three repetitions of each test signal recorded at 1 m that was not superimposed by transient noise fluctuations. Data analysis involved comparisons between filtered, degraded observation sounds, and their respective species-specific, undegraded control sounds. Quality of signal transmission was assessed *via* two measurements. Overall signal amplitude was used as a measure of attenuation over distance and spectrographic cross correlation (described below) served as a measure of distortion over distance.

Spectrograms were created for each of the signals using a transform length of 256 points and cross correlation analysis performed on these. Control and observation signals were aligned at the start, the two signals slid past each other, and a correlation coefficient calculated for each point in time based on both temporal and amplitude differences between the two calls. The maximum cross correlation coefficient obtained from each comparison was plotted against recording distance for each species in each habitat type and height. A curve was then fitted to each of these 84 plots and the values of the slopes of the curves used in subsequent analyses. Because data were normally distributed, three-way analysis of variance (ANOVA) was used to test for differences in signal transmission, with broadcast habitat, native habitat and recording height as independent variables.

Signal attenuation was analyzed by measuring the average intensity for each signal and then plotting this value against recording distance in a similar manner to that described above. The slopes of the curves were again used to evaluate differences in signal transmission.

In addition, ANOVAs were used to analyze both cross correlation coefficients and amplitude at the maximum
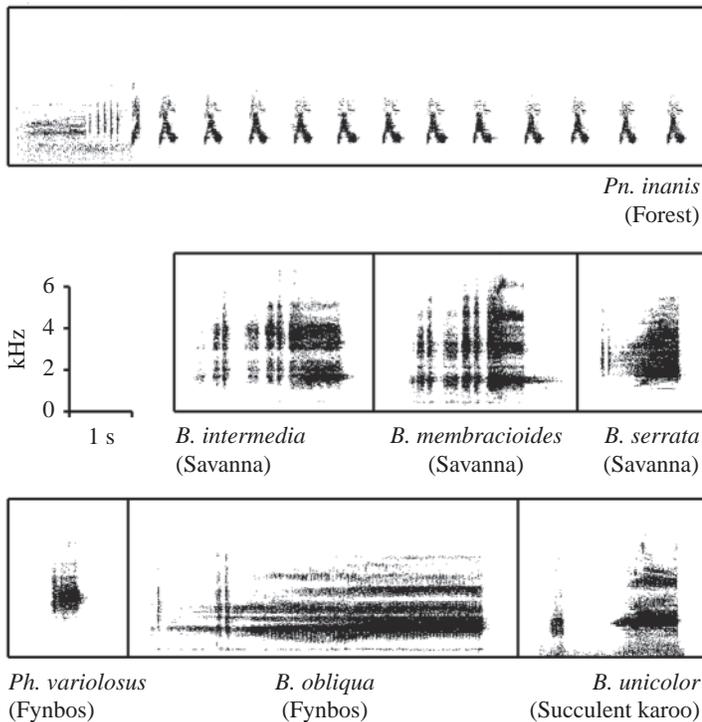

Fig. 2. Sonogram exemplars of species-specific male mate location signals for seven bladder grasshopper taxa used in the transmission experiments.

recording distance of 100 m, to assess differences among species within each vegetation biome. Due to the logarithmic nature of the dB scale, amplitude values in dB were converted into sound pressure values for the analysis and then converted back into dB.

Standard deviations (S.D.) of both cross correlation and intensity data were used to assess consistency of signal transmission. No significant differences in consistency (S.D.) were detected among any species for either cross correlation or intensity, and data from all species were therefore pooled to examine differences among habitats, using ANOVAs.

Environmental noise was estimated separately in each habitat by compiling 10 s of uncorrupted background noise from the silence between consecutive test sounds. From these, power spectra were derived representing background noise along the entire transect throughout the experimental session.

Results

A total of 3024 recorded signals were digitized for analysis, of which 204 (6.7%) were excluded from the data set due to transient noise fluctuations. Consequently, there were sometimes less than the maximum of six repetitions of each signal at each distance and height combination.

Distortion of transmitted grasshopper calls

There was a significant interaction between native habitat (the resident habitat of the pneumorid producing the call) and broadcast habitat (the habitat in which the call was broadcast) in the three-way ANOVA of spectrographic cross correlation, indicating that calls distort differently when broadcast in native versus non-native habitats (Table 2). In addition, there were marginally non-significant differences in broadcast habitat, recording height and the interaction between these two factors (Table 2). This suggests that call distortion varies independently according to both the habitat through which it is being transmitted and the height at which it is being transmitted, and that calls may transmit differently at given heights in different habitats.

Comparisons of cross correlation coefficients at a distance of 100 m revealed that the native forest species performed significantly better than all other species in the forest habitat at heights of both 1 m and 2 m, and significantly better than all except the succulent karoo species at a height of 0.2 m (Fig. 3A). In the fynbos (Fig. 3B), inhabitant species had significantly higher correlation coefficients than all other species at recording heights of 1 m and 2 m, although there were no significant differences at a height of 0.2 m. In their native habitat, savanna species outperformed the succulent karoo species at 0.2 m and 1 m heights, but fared significantly worse than fynbos species at 0.2 m and 2 m heights (Fig. 3C). Finally, in the succulent karoo, the indigenous species had significantly lower correlation coefficients than fynbos species at 0.2 m and 2 m, and than fynbos and savanna species at 1 m (Fig. 3D).

Attenuation of transmitted grasshopper calls

The habitat in which signals were broadcast, the native habitat of the grasshoppers, and the height at which signals were recorded all had a strongly significant effect on the amplitude of transmitted signals (Table 3). Height also had a significant interaction with broadcast habitat, indicating that calls attenuate differently in different habitats at similar heights.

Comparisons of amplitude measures at a maximum recording distance of 100 m are shown in Fig. 4. The call of the forest species attenuated significantly less in its native habitat than all other species at a height of 0.2 m, less than savanna and succulent karoo species at a height of 2 m, and less than savanna and succulent karoo species, but more than fynbos species, at a height of 1 m (Fig. 4A). Fynbos species had significantly higher amplitudes in the fynbos habitat than savanna and succulent karoo species at each of the three heights (Fig. 4B). Native species in the savanna had significantly lower amplitudes than forest and fynbos species at all three heights and significantly higher amplitudes than the succulent karoo species at 0.2 m and 1 m heights only (Fig. 4C). In the succulent karoo, the inhabitant species had

Table 2. *ANOVA on regression slopes of cross correlation coefficients over distance*

Source	d.f.	Sum of squares	*F*-ratio	*P*
Model	47	0.02648266	4.082	<0.001*
Broadcast Habitat	3	0.00174112	2.773	0.051
Native Habitat	3	0.00106951	1.704	0.178
Height	2	0.00083037	3.968	0.052
Broadcast × Native	9	0.00601000	3.191	0.004*
Broadcast × Height	6	0.00165911	2.643	0.059
Native × Height	6	0.00009435	0.150	0.929
Broadcast × Native × Height	18	0.00077820	0.413	0.922
Error	36	0.01088200		
Total	83	0.03736466		

*Significant, *P*<0.05.

Table 3. *ANOVA on regression slopes of signal amplitude over distance*

| Source	d.f.	Sum of squares	*F*-ratio	*P*
Model	47	341.68601	9.235	<0.001*
Broadcast Habitat	3	68.47082	28.991	<0.001*
Native Habitat	3	51.13323	21.650	<0.001*
Height	2	99.92324	63.463	<0.001*
Broadcast × Native	9	8.49397	1.199	0.326
Broadcast × Height	6	36.83090	7.797	<0.001*
Native × Height	6	5.53834	1.173	0.343
Broadcast × Native × Height	18	15.14157	1.069	0.418
Error	36	28.34117		
Total	83	370.02718		

*Significant, *P*<0.05.
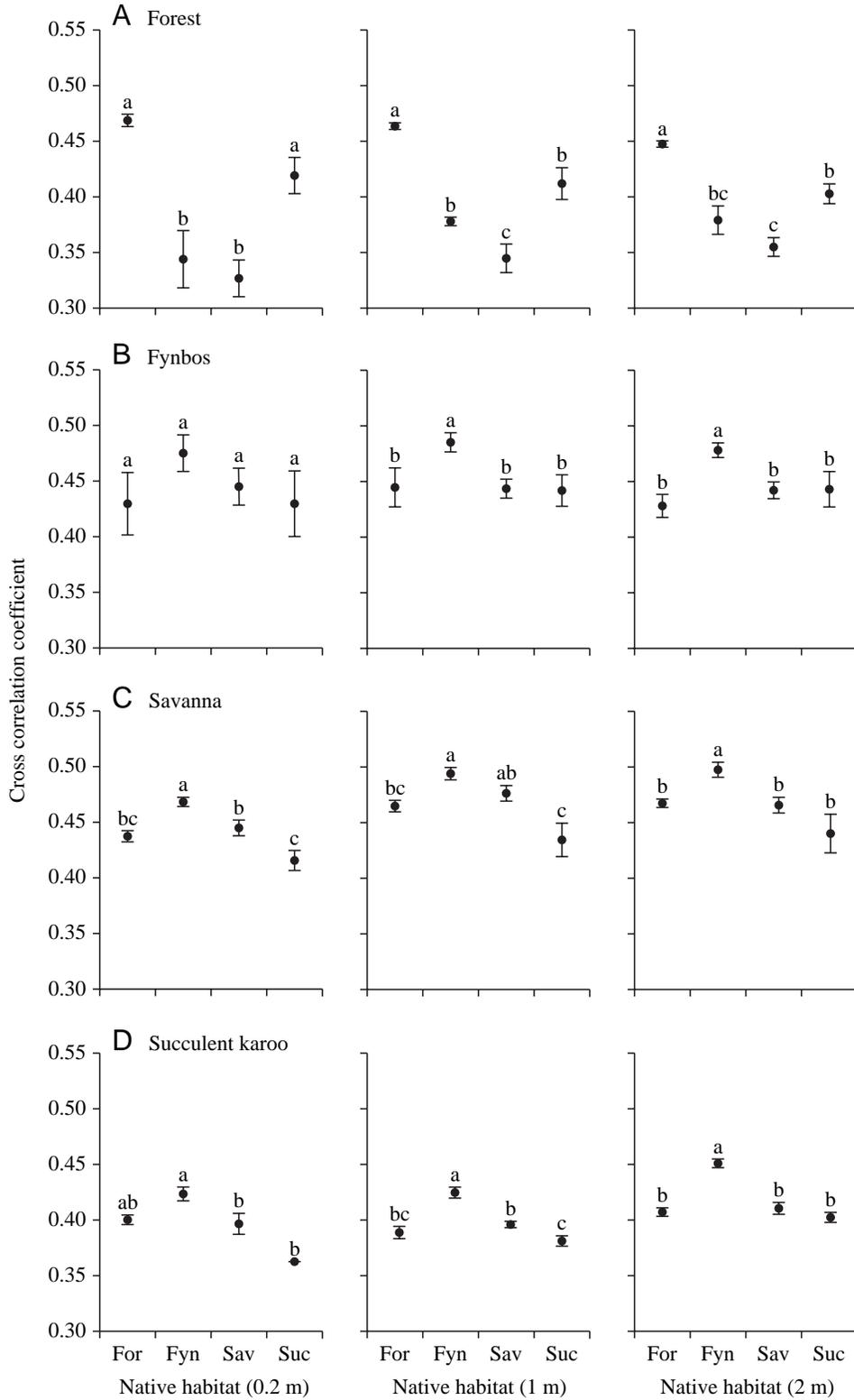
Fig. 3. Cross correlation coefficients (means ± S.E.M.) at a recording distance of 100 m in four transmission habitats and at three recording heights. Species are grouped according to their native habitats. Letters above error bars (a–c) indicate significance individually within each plot, with different letters representing a significant difference at the 5% level and the same letter indicating no significant difference.

among habitats ($F_{3,417}$=38.351; P<0.001; Tukey multiple comparison tests), with least variable distortion in forest and succulent karoo habitats, followed by the savanna and then by the fynbos (Fig. 5). Variation in sound distortion increased with distance from the speaker and as height above ground decreased. Consistency of signal attenuation also varied significantly among habitats ($F_{3,417}$=63.133; P<0.001; Tukey multiple comparison tests), with the highest consistency exhibited in the forest and the lowest in the fynbos (Fig. 6). Savanna and succulent karoo habitats were intermediate between these two and did not differ from each other. As expected, variation in attenuation was extremely low in the forest, and changed with neither recording distance nor height. In the other three habitats, consistency increased noticeably with distance at elevations of 1 m and 2 m. However, at 0.2 m recording height there was little or no relationship between standard deviation and distance.

Environmental noise

Levels of ambient background noise varied appreciably among localities (Fig. 7). Background noise in the forest was higher than in any other habitat and consisted mainly of the sounds of water running in nearby streams and of calling frogs. The savanna was also relatively noisy and was predominated by the songs of crickets and other insects. Both the fynbos and the succulent karoo appeared to have less background noise than the other two

significantly greater attenuation than forest and fynbos species at a height of 2 m, but showed no significant differences at both 0.2 m and 1 m heights (Fig. 4D).

Consistency of grasshopper calls
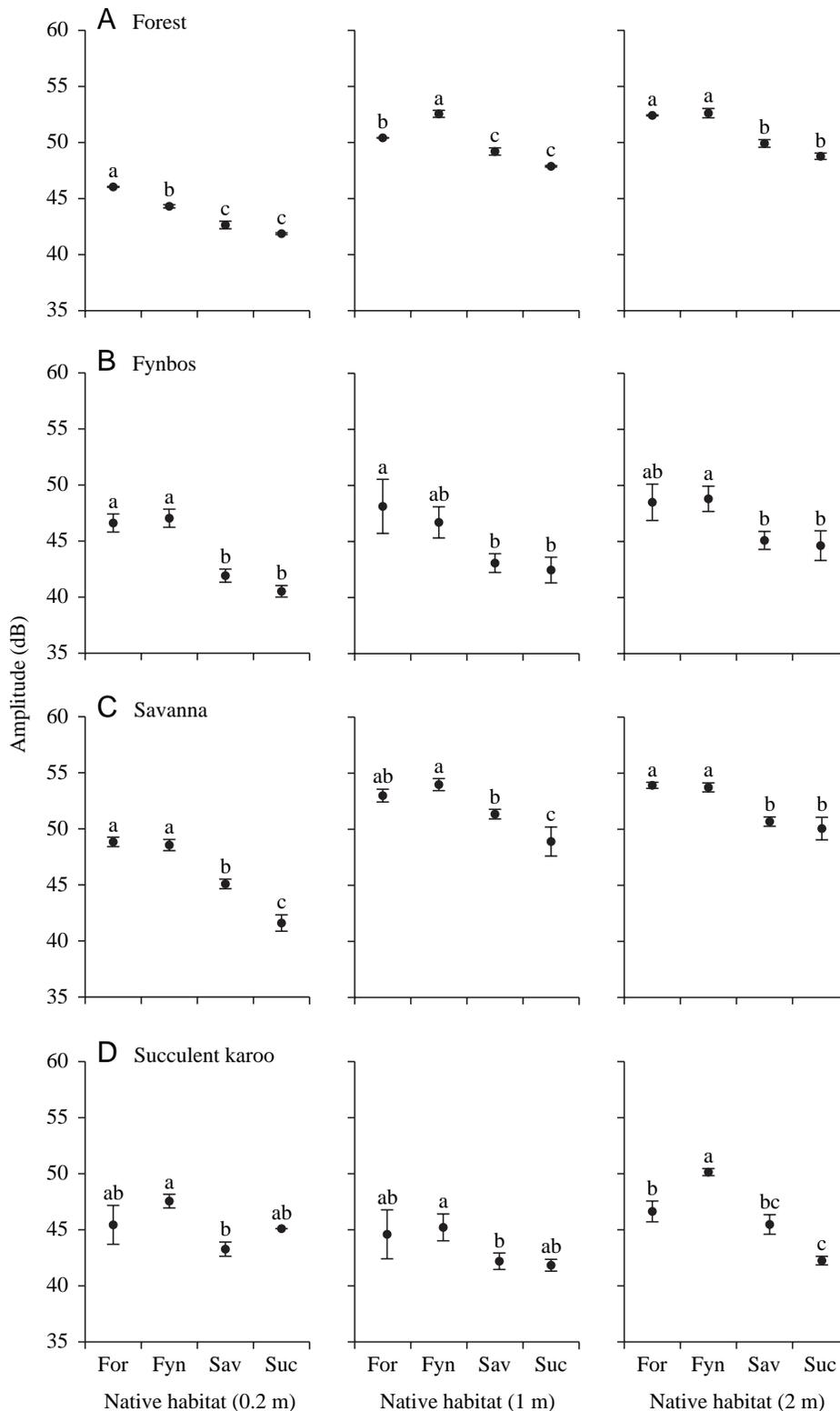
Consistency of signal distortion differed significantly

Fig. 4. Amplitude measurements (means ± s.e.m.) at a recording distance of 100 m in four transmission habitats and at three recording heights. At this distance, attenuation due to spherical spreading alone theoretically results in an amplitude of 56.4 dB. Species are grouped according to their native habitats. Letters above error bars (a–c) indicate significance individually within each plot, with different letters representing a significant difference at the 5% level and the same letter indicating no significant difference.

Discussion

Our results demonstrate that male bladder grasshopper advertisement calls transmit more favourably in native as opposed to non-native habitats, at least in some species. In accordance with the predictions of the acoustic adaptation hypothesis (Morton, 1975), native signals out-performed non-native signals in forest and fynbos habitats, but this finding did not hold for the savanna and succulent karoo habitats. Fynbos species performed consistently well in all environments except the forest in terms of signal distortion, whereas either forest or fynbos species predominated in most instances in terms of signal attenuation.

The pattern of performance of species' signals in the forest was distinctly different to that in the other three habitats, which all produced similar results. Although transmission in the savanna, fynbos and succulent karoo habitats yielded different levels of signal degradation, the relative relationship among species remained comparable. This may be explained in part by structural differences in the type of vegetation among the four habitats. Whereas the forest represents a closed habitat dominated by 5–25 m high trees and several understory layers, the other habitats are all more open with predominately low-lying vegetation (<1 m), sparsely interspersed with taller (1–2 m) shrubs. Moreover, while structural features are likely to be of greater import than floristic ones, it is notable that fynbos and succulent karoo biomes share 55% of their species diversity (Rutherford, 1997). It is therefore not surprising that at this level, our observations

habitats. The fynbos was mostly characterized by a few calling frogs and night birds, and the succulent karoo by the calls of insects. In addition, background noise in the forest was continuous, whereas in the other habitats it was intermittent.
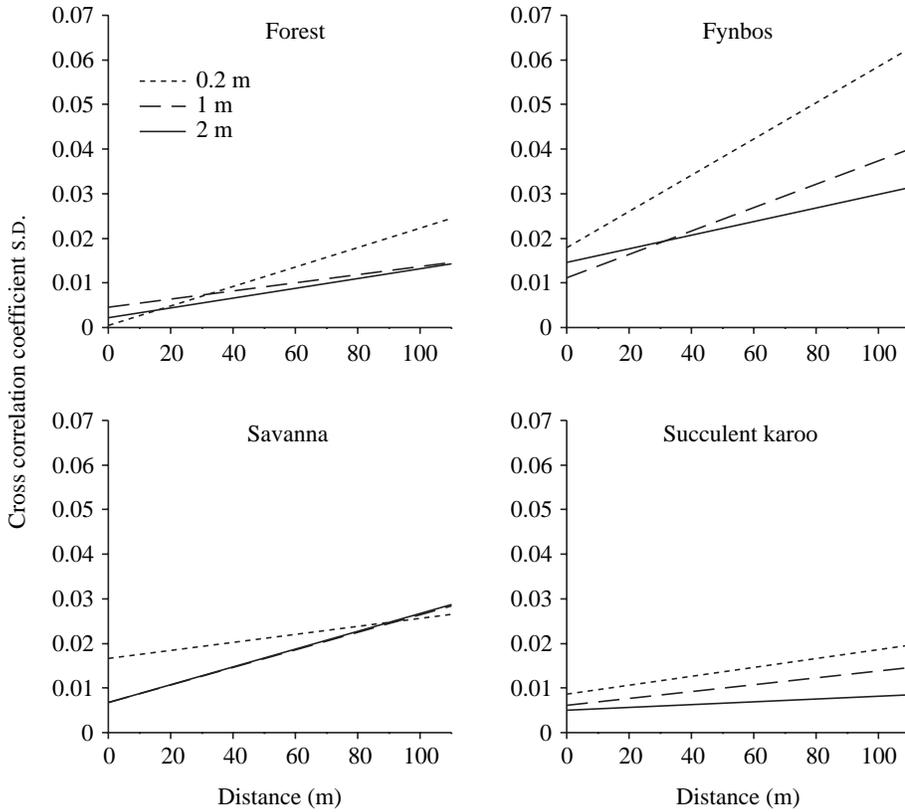
Fig. 5. Standard deviations of cross correlation coefficients plotted over distance at three different heights above the ground in four different habitats.
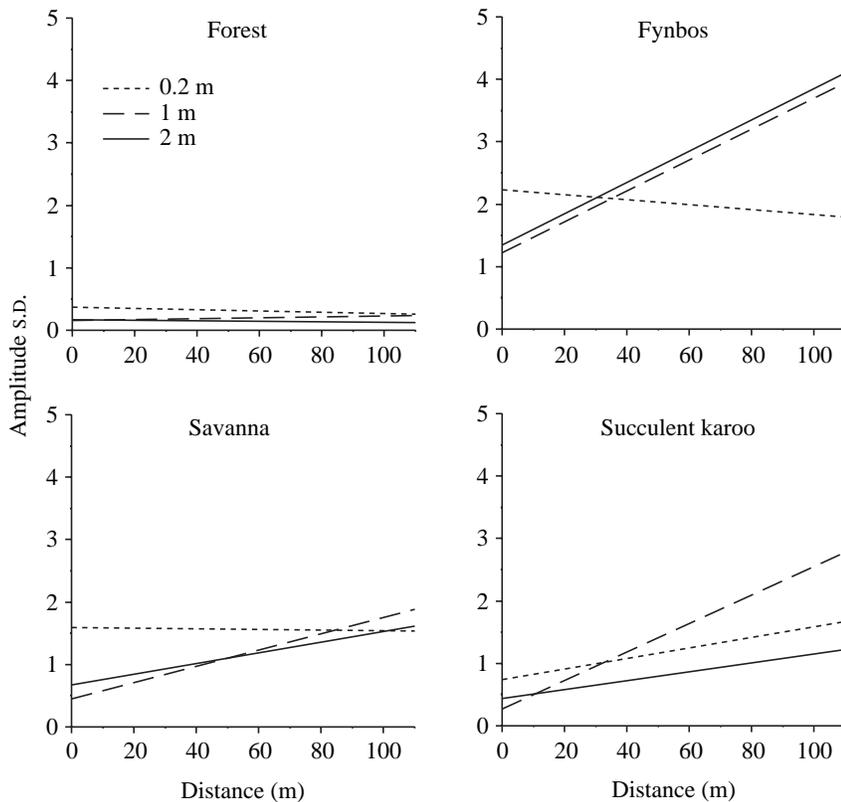

Fig. 6. Standard deviations of amplitude measurements (mean ± S.D.) plotted over distance at three different heights above the ground in four different habitats.

conform to expectations, with species performing similarly in the savanna, fynbos and succulent karoo, particularly at higher elevations, and performance in the forest differing significantly from that of the open habitats.

Recent studies have stressed the importance of broadcast variability as a critical consideration in the evolution of signals, perhaps even more so than broadcast quality (Brown and Handford, 2000, 2003). Although we found no differences in transmission variation among species, we did identify substantial differences among habitats. Interestingly, signal degradation in the fynbos was far more variable than in any other habitat and may provide an explanation as to why the calls of the native fynbos species performed admirably in all habitats. Selection pressure to maximize the reliability of information transfer in the signals of fynbos species potentially derives from two sources, *viz.* inherent characteristics of the transmission channel and inter-specific acoustic competition. The acoustic signals of native fynbos species are characterized by either relatively low-frequency calls, or very brief, high-frequency calls (Fig. 2), design features that could compensate for the lack of transmission reliability in their native habitat. In addition, pneumorid species diversity and sympatry achieve their highest levels in the fynbos habitat. The two fynbos species considered here are sympatric in at least part of their range, as well as with other pneumorid species not considered here (Dirsh, 1965). This temporal and spatial overlap means that males of several species may frequently call together in the same area, placing further selection pressure on the transmission channel to produce calls that can be clearly distinguished from those of heterospecifics. In light of this distribution overlap, fynbos species may have increased the transmission quality, rather than the consistency of their signals, and these features cannot simultaneously be maximized in open habitats (Brown and Handford, 2000).
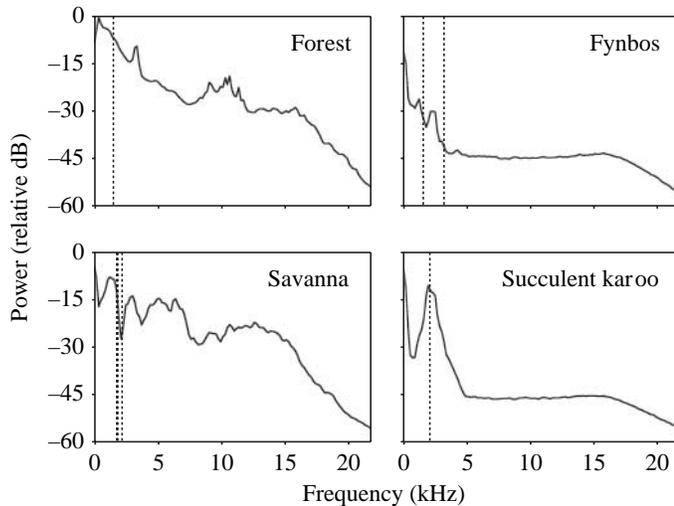
Fig. 7. Power spectra of environmental noise in the four different habitats where transmission experiments were performed. The dotted lines represent the carrier frequencies of the signals of species native to that habitat.

Height above ground level is an essential consideration in the transmission of sounds (Dabelsteen et al., 1993; Marten and Marler, 1977; Mathevon et al., 1996; Waser and Waser, 1977). We found cross correlation coefficients to be similar at all three heights, indicating that, in contrast to the situation with birds (Holland et al., 1998), elevation did not play a large role in signal distortion. Elevation did, however, have considerable impact on signal attenuation, which was much more pronounced closer to the ground. Consistency in signal propagation was also found to vary in accordance with height. Degradation was more variable at lower elevations and variation increased with distance at all three heights. Variation in attenuation tended to remain static at 0.2 m, but increased with distance at higher elevations. It should be noted that in our experimental design, the speaker was always kept at a constant height above the ground and only the position of the microphone was varied. It is likely that elevation would have had a much more pronounced effect had the broadcast height been adjusted in accordance with the receiver height.

The frequency dependency of the pattern of excess attenuation accumulation with transmission distance has been widely documented (Lang, 2000; Marten and Marler, 1977; Morton, 1975; Naguib, 1995). However, we found no significant correlation between call frequency and transmission in bladder grasshoppers. This lack of correlation was mostly due to the anomaly of *P. variolosus* emitting a comparatively high frequency signal, yet being one of the species with the highest transmission performances. Indeed, if *P. variolosus* is removed from the analysis, the relationship between call frequency and degradation becomes significant in the predicted direction. Furthermore, carrier frequency and call length are strongly negatively correlated in the species under examination here (Spearman Rho=–0.9643; *P*<0.001) and this relationship with call length may well be masking the effect of frequency

on call transmission, particularly in *P. variolosus*, which has an exceptionally short advertisement call. Reducing the duration of high frequency signals appears to be an effective adaptive mechanism to counteract degradation, irrespective of habitat type.

Ambient environmental noise is a form of acoustic interference that can mask signals in the same frequency range, and noise levels have previously been implicated in song divergence among populations within a species (Slabbekoorn and Smith, 2002). It is possible that environmental noise is placing selection pressure on bladder grasshoppers to avoid calling in the same frequency range as either other animals or abiotic factors in their local environment. Indeed, virtually all species tested here produced calls with peak frequencies mismatched to the dominant frequencies of ambient noise, from both biotic and abiotic sources, in their native habitats. The only exception was *B. unicolor* in the succulent karoo, which calls at a peak frequency that corresponds closely (within 200 Hz) with the most dominant frequency of background noise in its indigenous habitat. The precise source of this intermittent call is, as yet, unidentified, but the acoustic challenge the species presents for *B. unicolor* may constitute a telling exception to the apparent facility of bladder grasshoppers for maintaining a private communication channel.

Only thirteen species of bladder grasshopper have males displaying the primary morph of an inflated abdomen (Dirsh, 1965) and thus have the potential to produce long-distance mating signals. The seven species included in this study were those for which quality sound recordings are available, and represented the four vegetation types in unequal numbers of between one and three species per biome. This inequality and the lack of multiple representations of native species in two habitats are unfortunate, but unavoidable. Pneumorids are notoriously difficult to find in the field and the calls of six species have not yet been recorded. While a comprehensive picture of the effects of habitat acoustics on the evolution of male advertisement signals in this particular taxon would indubitably benefit by including some of the currently more elusive species, the present study demonstrates that signal structure varies among species in ways that reflect acoustically relevant differences in the environment. Different environments favour qualitatively different traits, thus supporting long-term evolutionary effects of habitat acoustics on signals and signalling behaviour (sensory drive; Endler, 1993).

The results presented here provide support in an invertebrate group for the acoustic adaptation hypothesis of covariance of acoustic signals and habitat characteristics in a manner that maximizes communication range. Moreover, they provide a bridge between the evolutionary history of the group and the ecological drive on the sensory system. A striking feature of the results is that while environmental selection explains some of the observed signal diversity of bladder grasshoppers, the effects of selection on species-specific advertisement calls are rather uneven. This discrepancy may be attributable in part to

variation in selection pressure; those species inhabiting environments less conducive to sound propagation over extended distances likely face stronger selection pressures to modify their signal characteristics in accordance with environmental properties. Furthermore, additional factors not considered here, such as female choice, male–male competition, density and variety of predators, and phylogenetic constraints, may all have had far-reaching impacts on signal evolution. The simultaneous coupling of these factors with environmental factors may account for the complex observed patterns of signal transmission.

References

Bennet-Clark, H. C. (1987). The tuned singing burrow of mole crickets. *J. Exp. Biol.* **128**, 383-409.

Bertelli, S. and Tubaro, P. L. (2002). Body mass and habitat correlates of song structure in a primitive group of birds. *Biol. J. Linn. Soc.* **77**, 423-430.

Bowman, R. I. (1979). Adaptive morphology of song dialects in Darwin's finches. *J. Ornithol.* **120**, 353-389.

Brown, C. H., Gómez, R. and Waser, P. M. (1995). Old World monkey vocalizations: adaptation to the local habitat? *Anim. Behav.* **50**, 945-961.

Brown, T. J and Handford, P. (2000). Sound design for vocalizations: quality in the woods, consistency in the fields. *Condor* **102**, 81-92.

Brown, T. J. and Handford, P. (2003). Why birds sing at dawn: the role of consistent song transmission. *Ibis* **145**, 120-129.

Castellano, S., Giacoma, C. and Ryan M. J. (2003). Call degradation in diploid and tetraploid green toads. *Biol. J. Linn. Soc.* **78**, 11-26.

Cosens, S. E. and Falls, J. B. (1984). A comparison of sound propagation and song frequency in temperate marsh and grassland habitats. *Behav. Ecol. Sociobiol.* **15**, 161-170.

Cowling, R. M., Richardson, D. M. and Mustart, P. J. (1997). Fynbos. In *Vegetation of Southern Africa* (ed. R. M. Cowling, D. M. Richardson and S. M. Pierce), pp. 99-130. Cambridge: Cambridge University Press.

Dabelsteen, T., Larsen, N. O. and Pedersen, S. B. (1993). Habitat induced degradation of sound signals: quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song. *J. Acoust. Soc. Am.* **93**, 2206-2220.

Dirsh, V. M. (1965). Revision of the family Pneumoridae (Orthoptera: Acridoidea). *Bull. Br. Mus. (Nat. Hist.) Entomol.* **15**, 325-396.

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**, S125-S153.

Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Phil. Trans. R. Soc. Lond. B* **340**, 215-225.

Forrest, T. G. (1994). From sender to receiver: propagation and environmental effects on acoustic signals. *Am. Zool.* **34**, 644-654.

Garstang, M., Larom, D., Raspet, R. and Lindeque, M. (1995). Atmospheric controls on elephant communication. *J. Exp. Biol.* **198**, 939-951.

Gish, S. L. and Morton, E. S. (1981). Structural adaptation to local habitat acoustics in Carolina wren song. *Z. Tierpsychol.* **56**, 74-84.

Handford, P. (1981). Vegetational correlates of variation in the song of *Zonotrichia capensis*. *Behav. Ecol. Sociobiol.* **8**, 203-206.

Hansen, P. (1979). Vocal learning: its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Anim. Behav.* **27**, 1270-1271.

Holland, J., Dabelsteen, T. and Pedersen, S. B. (1998). Degradation of wren *Troglodytes troglodytes* song: implications for information transfer and ranging. *J. Acoust. Soc. Am.* **103**, 2154-2166.

Keuper, A., Kalmring, K., Schatral, A., Latimer, W. and Kaiser, W. (1986). Behavioural adaptations of ground living bushcrickets to the properties of sound propagation in low grassland. *Oecologia* **70**, 414-422.

Kime, N. M., Turner, W. R. and Ryan, M. J. (2000). The transmission of advertisement calls in Central American frogs. *Behav. Ecol.* **11**, 71-83.

Lang, F. (2000). Acoustic communication distances of a Gomphocerine grasshopper. *Bioacoustics* **10**, 233-258.

Marten, K. and Marler, P. (1977). Sound transmission and its significance for animal vocalization I. Temperate habitats. *Behav. Ecol. Sociobiol.* **2**, 271-290.

Mathevon, N., Aubin, T. and Dabelsteen, T. (1996). Song degradation during propagation: importance of song post for the wren *Troglodytes troglodytes*. *Ethology* **102**, 397-412.

McComb, K., Reby, D., Baker, L., Moss, C. and Sayialel, S. (2003). Long-distance communication of acoustic cues to social identity in African elephants. *Anim. Behav.* **65**, 317-329.

Morton, E. S. (1975). Ecological sources of selection on avian sounds. *Am. Nat.* **109**, 17-34.

Naguib, M. (1995). Auditory distance estimation of singing conspecifics in Carolina wrens: the role of reverberation and frequency-dependent attenuation. *Anim. Behav.* **50**, 1297-1307.

Penna, M. and Solís, R. (1998). Frog call intensities and sound propagation in the South American temperate forest region. *Behav. Ecol. Sociobiol.* **42**, 371-381.

Rutherford, M. C. (1997). Categorization of biomes. In *Vegetation of Southern Africa* (ed. R. M. Cowling, D. M. Richardson and S. M. Pierce), pp. 91-98. Cambridge: Cambridge University Press.

Ryan, M. J., Cocroft, R. B. and Wilczynski, W. (1990). The role of environmental selection in intraspecific divergence of mate recognition signals in the cricket frog, *Acris crepitans*. *Evolution* **44**, 1869-1872.

Shy, E. and Morton, E. S. (1986). Adaptation of amplitude structure of songs to propagation in field habitat in song sparrows. *Ethology* **72**, 177-184.

Slabbekoorn, H. and Smith, T. B. (2002). Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. *Evolution* **56**, 1849-1858.

van Staaden, M. J. and Römer, H. (1997). Sexual signaling in bladder grasshoppers: tactical design for maximizing calling range. *J. Exp. Biol.* **200**, 2597-2608.

van Staaden, M. J. and Römer, H. (1998). Evolutionary transition from stretch to hearing organs in ancient grasshoppers. *Nature* **394**, 773-776.

Waser, P. M. and Brown, C. H. (1986). Habitat acoustics and primate communication. *Am. J. Primatol.* **10**, 135-154.

Waser, P. M. and Waser, M. S. (1977). Experimental studies of primate vocalization: specializations for long-distance propagation. *Z. Tierpsychol.* **43**, 239-263.

Wiley, R. H. (1991). Associations of song properties with habitats for terrestrial oscine birds of eastern North America. *Am. Nat.* **138**, 973-993.

Wiley, R. H. and Richards, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: implication for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* **3**, 69-94.

Wollerman, L. (1999). Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*. *Anim. Behav.* **57**, 529-536.

Yack, J. E., Otero, L. D., Dawson, J. W., Surlykke, A. and Fullard, J. H. (2000). Sound production and hearing in the blue cracker butterfly *Hamadryas feronia* (Lepidoptera, Nymphalidae) from Venezuela. *J. Exp. Biol.* **203**, 3689-3702.

Zimmerman, B. L. (1983). A comparison of structural features of calls of open and forest habitat frog species in the central Amazon. *Herpetol.* **39**, 235-246.