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Abstract. Animal vocalizations used for long-distance communication are shaped by acoustic properties of the environment. Studies of the relationship between signal design and sound transmission typically focus on habitat-induced limitations due to signal attenuation and degradation. However, signal design may not entirely be explained by habitat limitations, but rather by beneficial consequences of reverberations. Narrow-frequency bandwidth notes (NFB notes) are pure notes that change little in frequency, and are typical for many bird species living in dense tropical forests. In contrast to frequency-modulated notes, we show that reverberations lead to a longer and louder signal after transmission for NFB notes. Furthermore, playback experiments to territorial males of an African passerine indicated that longer notes led to a stronger behavioral response. These results suggest that reverberations may benefit signal efficiency depending on the signal design, and add new insight into the selection pressures imposed on acoustic signals by the environment.

Key words: acoustic design, birdsong, convergence, Green Hylia, Hylia prasina, sound transmission.

Canto de Aves y Transmisión de Sonido: Beneficios de las Reverberaciones

Resumen. Las vocalizaciones utilizadas por animales para la comunicación a larga distancia están condicionadas por las propiedades acústicas del entorno. Los estudios sobre la relación entre el diseño de las señales y la transmisión del sonido suelen centrarse en los límites impuestos por el hábitat debido a la atenuación y degradación de la señal. Sin embargo, es posible que el diseño de la señal no esté regido exclusivamente por las limitaciones del habitat, sino por las consecuencias beneficiosas de las reverberaciones. Las notas de frecuencia de banda estrecha (notas NFB) son notas puras que cambian poco de frecuencia y son típicas de varias especies que habitan bosques tropicales densos. Al contrario que en las notas de frecuencia modulada, mostramos que las reverberaciones alargan y aumentan la señal de las notas NFB. Asimismo, experimentos de playback con machos territoriales de un paseriforme africano indican que las notas más largas provocan una mayor respuesta. Estos resultados sugieren que las reverberaciones pueden mejorar la eficiencia de la señal, dependiendo del diseño de la misma, y añaden un nuevo componente a nuestro conocimiento sobre las presiones selectivas impuestas por el entorno sobre las señales acústicas.

INTRODUCTION

Animal vocalizations designed to maximize or optimize transmission distance are shaped by acoustic properties of the environment (Wiley and Richards 1978, Endler 1992, Forrest 1994). As a consequence, species living in one particular habitat may show convergence in general acoustic features due to shared selection pressures. Numerous studies have yielded a set of general acoustic features associated with habitat characteristics (Chappuis 1971, Morton 1975, Ryan and Brenowitz 1985, Sorjonen 1986, Wiley 1991, Badyaev and Leaf 1997). Typically, songs in open habitat are characterized by relatively high frequencies and a wide frequency range, consisting of complex notes, produced with short internote intervals, often in the form of trills. By contrast, songs in dense forests are characterized by relatively low frequencies and a narrow frequency range, consisting of long and simple notes. In addition, tropical forest birds often use individual notes concentrated within an extremely narrow-frequency bandwidth
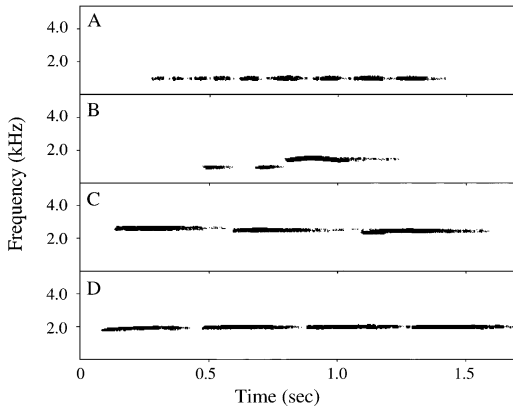
FIGURE 1. Four examples of song with narrow-frequency-bandwidth notes in songs of typical bird species of dense tropical forest in Central Africa. (A) Blue-headed Crested Flycatcher (*Trochocercus nitens*). (B) Black-headed Oriole (*Oriolus brachyrhynchus*). (C) Yellow Longbill (*Macrosphenus flavicans*; partial song). (D) Chocolate-backed Kingfisher (*Halcyon badia*; partial song).

(NFB). The same NFB notes, with an almost constant frequency throughout the note (Fig. 1), are found across taxonomic groups, and can be heard in tropical forests around the world (Africa: Chappuis 1971; Central America: Morton 1975; Asia: HS, pers. obs.).

Important factors driving habitat-dependent convergence are signal attenuation and degradation during sound transmission. Attenuation refers to amplitude decrease and is caused in part by absorption and scattering due to vegetation. Signal degradation refers to any change in spectral, temporal, and structural characteristics occurring between sender and receiver. The degree and nature of attenuation and degradation depend on vegetation characteristics of the habitat (Aylor 1971, Marten et al. 1977, Martens 1980, Price et al. 1988). Typically, sound heard by a receiver has traveled via many different pathways due to the scattering of sound waves by the vegetation. The scattered sound waves have longer pathways and, besides causing irregular amplitude fluctuations throughout the note, give rise to an echo, or a ''tail'' of sound following the sound received via the most direct pathway. Many studies to date have investigated the consequences on acoustic communication of these reverberations (Wiley and Richards 1978, 1982, Richards and Wiley 1980, Michelsen and Larsen 1983, Ryan and Sullivan 1989, Brown

and Handford 1996, 2000). These studies have yielded a detailed understanding of many aspects related to the detrimental impact of reverberations on signal efficiency. In addition, there are also indications that birds can use reverberations as a distance cue, which may be advantageous to sender and receiver (McGregor and Krebs 1984, Naguib 1996, Naguib et al. 2000).

Reverberations affect the spectral degradation of song notes in a way that depends on the frequency change or slope of the note. For a typical frequency-modulated note, a signal receiver will hear the frequency of the most direct sound wave, but at the same time also scattered sound waves of different frequencies, which are echoes of the preceding part of the note (Fig. 2A). This leads to the presence of delayed lower frequencies for upward slopes, and the presence of delayed higher frequencies for downward slopes. In contrast, for NFB notes, the delayed sound waves are all of the same frequency, and do not lead to spectral degradation. In addition to this qualitative distinction between NFB notes and frequency-modulated notes, we hypothesize that the tail following the last direct sound wave will be longer and louder for NFB notes, due to accumulation of scattered sound waves of the same frequency. As a consequence of the longer and louder signal for the same amount of energy, reverberations may assist the bird in transmitting its song. We suggest that such a benefit may have contributed to the convergence of song with NFB notes, explaining why species in dense habitats have similarly structured songs.

In order to test how NFB notes are affected by transmission through dense vegetation, we recorded songs of the Green Hylia (*Hylia prasina*), an African passerine that inhabits dense tropical rainforest. The song of the Green Hylia is very simple and consists of two successive NFB notes of the same frequency. We also recorded artificially generated tones, which avoided the problem of uncertainty about the acoustic characteristics of the signal before transmission at the bird's beak, and enabled us to test the influence of slope of the note on degradation during transmission. Additionally, we used artificial songs of different duration in playbacks to measure the behavioral response of Green Hylia in the field. In this way, we tested whether a song consisting of NFB notes with extended duration could be beneficial to the sender.
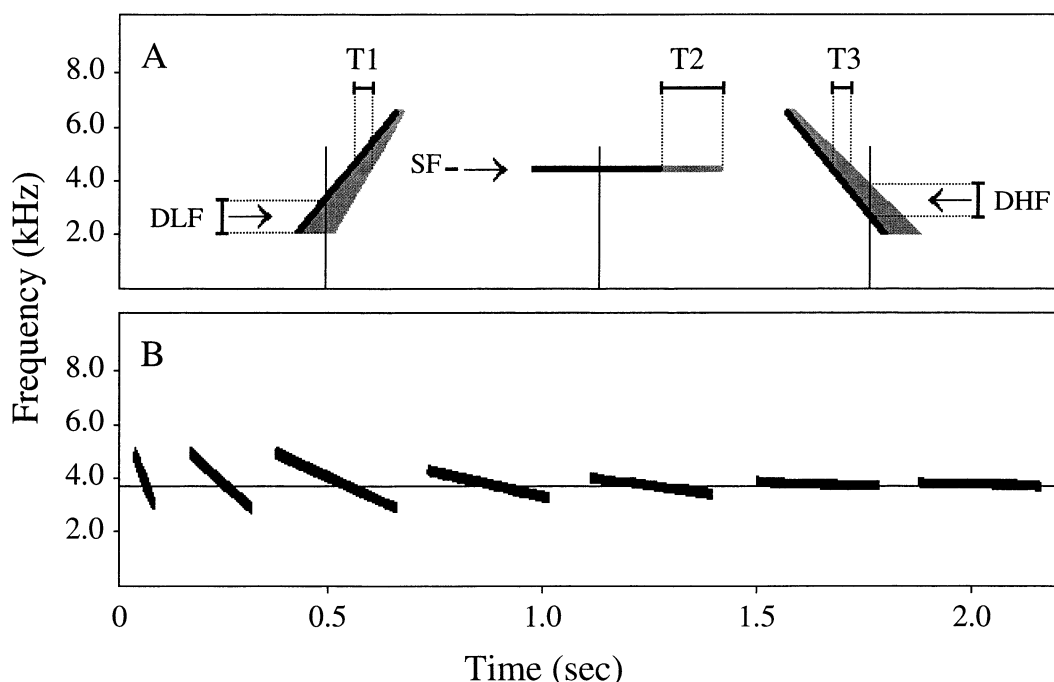
FIGURE 2.   (A) The effect of reverberations on three tones: one with an upward frequency slope, one with a narrow-frequency bandwidth (NFB), and one with a downward frequency slope. Black represents sound received via the direct pathway; gray is delayed sound received via indirect pathways. The three solid vertical lines indicate time slices, which show that reverberations lead to qualitative differences for the three notes: delayed lower frequency sound (DLF) for upward slopes, delayed higher frequency sound (DHF) for downward slopes, and direct and delayed sound all at the same frequency (SF) for NFB tones. Accumulation of SF sound also leads to a longer tail (T2) for NFB tones, compared to the tails of frequency-modulated tones (T1, T3). Note that tail duration varies throughout frequency-modulated tones due to frequency-dependent attenuation. (B) Schematic representation of the artificial stimuli set used for the transmission experiment. The slopes vary from left to right, from $-30\,000$ to -150 Hz sec^{-1}. Positive slopes, not shown, are the mirror image of the negative slopes. Green Hylia song notes have negative slopes of <300 Hz sec^{-1}, comparable to the two shallowest slopes on the right. The horizontal line at 3800 Hz indicates the frequency used for tail measurements.

METHODS

STUDY SITE AND RECORDINGS

Field research was conducted from January to April 1999, in humid tropical forest in Cameroon, central Africa. Recordings, transmission experiments, and playbacks were conducted in the Réserve de Dja (3°11′N, 12°49′E; Whitney et al. 1998). We recorded songs of Green Hylia using territory maps to avoid sampling the same individual twice. The estimated distance between subject and microphone varied between 5 and 30 m. Singing individuals were often very active, and moving through their territory. Locations and flight pathways of singing individuals were indicated on a map, and we observed what we thought were the same individuals on two different days. The distance between two map locations for the same individual was on average 64 ± 58 m (SD, $n = 24$). The average distance between map locations of two singing neighbors was 163 ± 89 m ($n = 35$).

TRANSMISSION EXPERIMENT

To investigate transmission characteristics, we recorded a series of artificial sounds after transmission through natural vegetation. The set of artificial tones was designed to test whether the tail formation after a tone depends on the frequency slope of the tone. The stimulus set consisted of 14 tones of 100 to 300 msec (Fig. 2B), which were of equal amplitude throughout the tone with short 10-msec ramps for smooth onset and end of playback. All tones had a constant frequency change, but with variable slopes:

−30 000, −15 000, −6750, −3400, −1700, −300, −150, 150, 300, 1700, 3400, 6750, 15 000, 30 000 Hz sec^{-1}. The tones were played back and recorded at heights of 3 m, and the transmission transect was 16 m through undergrowth foliage. We chose the height of 3 m to represent perching height of birds singing in undergrowth, and at the same time to reduce the impact of the ground on signal transmission (Aylor 1971, Marten et al. 1977). We expected 16 m to be long enough for significant accumulation of reverberations. Green Hylias may experience even a stronger impact of reverberations, as they presumably communicate over longer distances. All artificial tones were transmitted and recorded twice to reduce the impact of irregular amplitude fluctuations. Signal-to-noise ratios were measured throughout the experiment to check whether background noise levels could have influenced our tail measurements. Sound pressure level of playback was 68.5 dB on average, measured at 1 m from the speaker with a background noise of 45.5 dB (IE-30A SPL meter; Ivie Technologies, Lehi, Utah).

ACOUSTIC MEASUREMENTS

Recordings of songs and artificial sounds were digitized at a sampling frequency of 25 000 Hz, and spectrograms were generated via a standardized procedure (fast Fourier transformation size 512). The measurements of Green Hylia song included onset and end of notes, end of tail, peak frequency, frequency slope, and peak amplitude over the total duration of the double-noted song. In addition, we took amplitude measurements of the song (S), the tail (T), and the background noise (N). We used a programmed routine for automatic amplitude measurements at four points in the song: 50 msec before and after onset of the first song note, and 50 msec before and after the end of the second song note. Onset and end of notes were determined by cursor placements on the spectrogram, which was difficult for the latter due to the reverberations: cursor placement was based on the continuous trace on the spectrogram in combination with the pattern of the amplitude oscillogram (Fig. 3A, B). Amplitude levels were determined over a 10-msec period, for S, T, and N, all at the same frequency, determined by the frequency of peak amplitude of the song. The measurements were subsequently transformed to values relative to the peak amplitude, leading to values from 0 to 1.

The measurements of the artificial tones were essentially the same as for the Green Hylia songs. Amplitude measurements were taken at three locations to assess signal-to-noise ratio (S/N) and relative tail amplitude (T/S). One measurement was taken on the stimulus slope (S), determined by cursor placement on the spectrogram, while two measurements were taken 50 msec before (N), and 50 msec after (T) that location on the slope. N and T were located automatically based on the cursor placement for S. The cursor was placed at the end of the note for the two most shallow slopes (using reference to the signal onset of these tones of known length, which was always clear on the spectrogram), while N was measured at 50 msec before signal onset, as the measurements would otherwise fall within the tone for these slopes. The measurements were always taken at the same frequency (3800 Hz), irrespective of the steepness of the slope.

PLAYBACK EXPERIMENT

Two different artificial stimuli were played to individual Green Hylia on their territories. The two stimuli were imitations of the natural double-noted song, based on acoustic measurements of 53 recordings from 22 individuals. Both songs had a constant frequency of 3724 Hz, but differed in note duration. The first (''normal'') stimulus had the following durations for note one, interval, and note two: 285, 70, and 265 msec, which were the population averages for these song components. The second stimulus was an ''extended version,'' generated by adding two SD to the length of each note. This led to an extension of total song duration and a reduction in interval duration: 345, 15, and 315 msec.

Each note was created with 50-msec ramps for gradual sound onset and end and with equal amplitude for the remaining part of the note. After transmission, the amplitude patterns for both of the artificial song stimuli were affected by natural reverberations (Fig. 3C, D). The amplitude incline and decline over the two notes became even more gradual, presumably through accumulation of reflected sound of the same frequency. Furthermore, an irregular pattern of amplitude fluctuations was superimposed on the primary amplitude wave, leading to less distinct changes from sound that traveled the direct pathway to the reflected ''sound tail.'' Thus, both
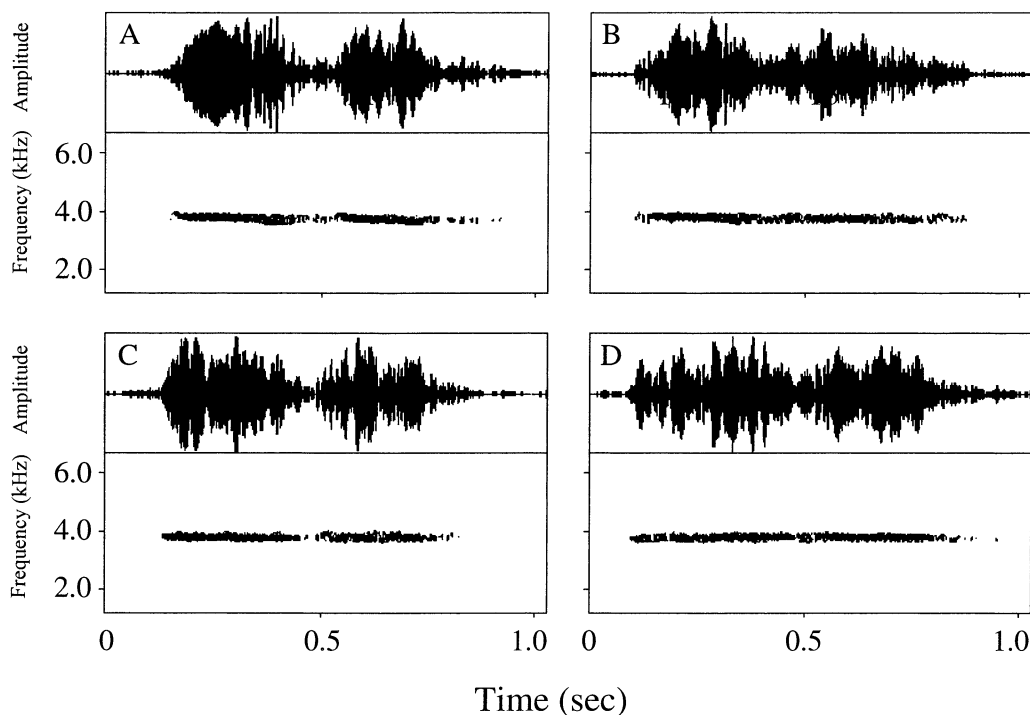
FIGURE 3.   Spectrograms and amplitude oscillograms of natural Green Hylia song and artificial song stimuli used for the playback experiment. (A) Green Hylia song recorded at ca. 5 m and (B) Green Hylia song recorded at ca. 12 m. Note that the two songs (recordings of the same individual) differ in amplitude pattern, with sound filling the note interval more completely in the more distantly recorded song. (C) Artificial song of normal duration, recorded at ca. 4 m from the speaker in the rainforest during a playback experiment, and (D) artificial song of "extended" duration, also recorded at ca. 4 m during the same experiment. The irregular pattern of amplitude fluctuations would be different for every new playback location and for every position of the microphone (or bird). The amplitudes of all four recordings were normalized, to remove absolute differences between the recordings.

stimuli were reverberated, but differed in duration of notes and intervals.

Natural song recordings are inherently affected by reverberations and would lead to doubly reverberated stimuli if used for playback. We also avoided a problem of pseudoreplication by using one set of artificial stimuli (with measurements based on population averages), instead of recordings of one or two individuals (see Kroodsma 1989, McGregor et al. 1992). Therefore, our findings can be attributed to song duration and not to an anomaly in the song of one particular individual.

The experimental procedure lasted 6 min: 2 min without any playback, 2 min of observation on the response to the first stimulus, and 2 min of observation on the response to the second stimulus. Playback consisted of five repetitions of the double-noted song at the start and end of

the third minute and at the start and end of the fifth minute, leading to a total of 20 repetitions throughout the procedure. Experiments were conducted in 12 territories; 6 of these received the normal stimulus first, and 6 received the extended version first. Such a balanced experimental design limits the impact of a carry-over effect (Slabbekoorn and ten Cate 1998).

The speaker was placed in the undergrowth, directed toward the subject, at 1 to 2 m height on a branch or suspended between twigs. We used a 6-m extension cable allowing the observer to stand away from the sound source. In pilot experiments Green Hylia males typically responded by approaching the speaker while increasing their vocalization rate. Individuals were rarely seen during a playback procedure, which made a quantification of approach distance, or any other behavioral response besides vocaliza-

tions, impossible. We scored two vocalization types, the double-noted song and a ''chutter'' call, which is a rapid trill of short notes with a wide frequency bandwidth. We analyzed the number of vocalizations in each of the periods and tested whether they responded more during playback compared to pre-playback, and whether they responded differently to the two stimuli. We expected the extended stimulus to signal an intruder of higher threat, such as a higher quality competitor capable of producing a longer signal (for a review on acoustic signaling of quality in male-male competition, see ten Cate et al. 2001). Consequently, we predicted that this stimulus would trigger a stronger vocal response.

EQUIPMENT

Recordings of birdsong and artificial stimuli after transmission were made with a Sennheiser ME67 directional microphone and a Sony TCM-5000EV tape recorder, using TDK SA90 tapes. Stimuli in transmission and playback experiments were played using a Sony TC-D5M tape recorder with a Sony SRS-A45 Active Speaker. All songs and stimuli were recorded with the same equipment, and therefore, differences in acoustic measurements were fully attributed to the associated acoustic design. We used AVI-SOFT software (Version 3.4d, Specht 1998) for preliminary analyses of song characteristics, and for generation of artificial stimuli. Automatic and onscreen acoustic measurements were taken with programmed routines for SIGNAL software (Version V3.05, Engineering Design 1997). Results are presented as means ± SD.

RESULTS

TRANSMISSION EXPERIMENT

The transmission of artificial tones with varying slopes through 16 m of foliage led to tail durations ranging from 72 to 353 msec (Fig. 4A), with relative tail amplitudes between 0.07 and 0.67 (Fig. 4B). Two-way ANOVA, with slope and sign of slope as factors, revealed a significant effect of slope for tail duration and tail amplitude, but no effect of sign of slope. The shallower slopes had longer and louder tails, while there was no significant variation in signal-to-noise ratio related to slope or sign of slope (Fig. 4C). Tukey HSD post-hoc comparisons showed that the notes with shallow slopes of 150 and 300 Hz sec^{-1} had significantly longer tails compared to any steeper slope (all $P < 0.01$). The
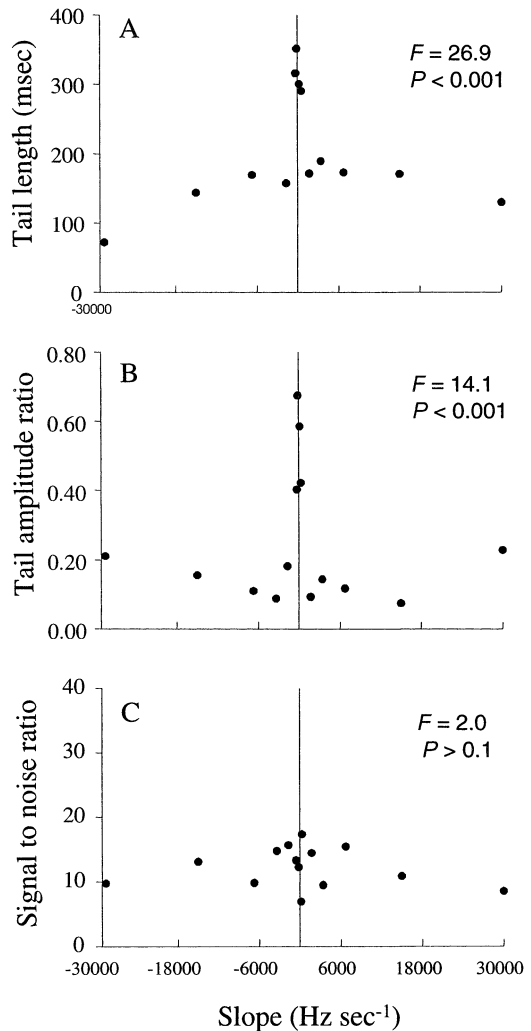

FIGURE 4. Impact of frequency slope on tail characteristics after transmission of artificial tones. (A) Slope versus tail duration, (B) slope versus relative tail amplitude, and (C) slope versus signal-to-noise ratio. Test statistics refer to the effect of slope (150–30 000 Hz sec^{-1}) in 2-way ANOVAs; the effect of sign of slope was never significant (all $P > 0.1$).

tail lengths of slopes 1700 to 15 000 Hz sec^{-1} were not significantly different, and the tail of 30 000 Hz sec^{-1} was significantly shorter than all other slopes (all $P < 0.05$). Similarly, the tail amplitude was significantly higher for the two shallowest slopes, compared to all other steeper slopes (all $P < 0.05$; this was true at 50 msec, but also if measured at 100 msec into the tail). The tail amplitude did not differ significantly among slopes 1700 to 30 000 Hz sec^{-1} ($P >$

TABLE 1. Response of Green Hylia to playback: the average number of chutters and songs ($\pm$ SD) during playback of artificial stimuli. "Normal" refers to an artificial song with note and interval durations based on population averages. "Extended" refers to an artificial song with note durations elongated by two standard deviations. "Difference" stands for the average difference ($\pm$ SD) between the responses to the two stimuli. Test statistics are given for the Wilcoxon signed-ranks test ($n = 12$).

	Normal	Extended	Difference	Z	P
Chutter	3.5 $\pm$ 3.7	4.6 $\pm$ 4.0	1.1 $\pm$ 0.8	−2.7	0.0006
Song	2.8 $\pm$ 2.5	3.4 $\pm$ 2.4	0.7 $\pm$ 0.9	−2.1	0.03

0.1). These results show that artificial tones with shallow slopes (equal to or less than 300 Hz sec^{-1}) give rise to longer and louder tails after transmission than any steeper slope, irrespective of whether it is an upward or downward slope.

SONG OF GREEN HYLIA

We recorded 120 songs of 24 individuals (five songs per individual) of the Green Hylia. Averages for individuals were used to calculate overall averages for the species. The mean peak frequency was 3788 $\pm$ 64 Hz, while the double-noted song showed a very small frequency decrease of −133 $\pm$ 61 Hz sec^{-1} (range −262 to 33.2 Hz sec^{-1}). The two notes were 279 $\pm$ 38 and 261 $\pm$ 42 msec in duration respectively, with an internote interval of 105 $\pm$ 37 msec. The interval always showed a tail of the first note reaching into the second note. The tail following the second note was of considerable duration: 362 $\pm$ 94 msec, varying from 164 to 577 msec. Tail amplitudes were often as loud as, and sometimes even louder than, the amplitudes measured within the signal (expressed as proportion of the peak amplitude of the song). The average amplitude of the tail (T/S) was 0.16 $\pm$ 0.06; the average amplitudes measured at the end of the preceding note and at the beginning of the first note were 0.33 $\pm$ 0.11, and 0.43 $\pm$ 0.13 respectively, while the average amplitude of the background noise (N/S) was 0.08 $\pm$ 0.06.

PLAYBACK EXPERIMENT

Territorial individuals of the Green Hylia responded to the playbacks with chutter calls and double-noted songs in all 12 experiments. In the pre-playback period the average number of chutters was 1.1 $\pm$ 1.0, and the average number of songs was 1.3 $\pm$ 1.4. The number of chutters and the number of songs both increased from the pre-playback period to the playback period: $Z = -2.8$, $P < 0.01$, and $Z = -2.4$, $P < 0.02$

respectively ($n = 12$, both stimuli combined, Wilcoxon signed-ranks test). This indicated that the birds did respond to the playbacks, which suggests our experiments successfully mimicked the presence of a natural competitor. Furthermore, individuals responded more strongly to the extended stimuli, both with chutter calls and double-noted songs (Table 1). This showed that the two stimuli are perceived differently, and tones of longer duration are significantly more effective in eliciting a response.

DISCUSSION

This study shows that transmission properties of dense vegetation can lead to degradation of animal vocalizations that is not detrimental, but may enhance signal effectiveness. Accumulation of reverberations at the same frequency led to longer and louder tails for artificial NFB tones in a transmission experiment. Analyses of Green Hylia songs indicated that natural NFB notes are affected by transmission in the same way as artificial tones. An accumulation of reverberations filled internote intervals and extended notes with a significant tail. By avoiding frequency modulation, they produced a longer and louder signal for the same amount of energy. Playback of artificial song to Green Hylia males indicated that longer notes are more effective in triggering a response, and may be beneficial to the birds in defending a territory or in attracting mates. Therefore, our findings suggest that by using NFB notes vocalizing animals can exploit the sound transmission properties of their environment.

Increase of note duration is one aspect among several that differ between reverberated and unreverberated song. Due to the omnipresence of reflective surfaces affecting all sounds in the forest, it is impossible to expose birds to unreverberated song in their natural environment. However, it is possible to test the impact of song

duration, which is what we did. Although we do not know the Green Hylia song characteristics at the bird's beak, naturally reverberated artificial songs used in the playbacks were very similar to naturally reverberated Green Hylia song. We cannot exclude the possibility that the birds are able to distinguish artificial and natural reverberated song, but they do respond differently to short and long versions of artificial song. Two possible explanations for the stronger responses in the playback experiment are (1) they are caused by an increased detectability of the longer signal, and (2) they are due to the receivers perceiving the longer signal as more threatening, as if it were a signal produced by a stronger competitor. The latter explanation calls for an examination of the relationship between sender characteristics and song duration (cf., Appleby and Redpath 1997).

In addition to the accumulation of reverberations, other factors can also affect the selection pressure on the use of NFB notes in tropical dense forest. Concentrating energy within a narrow-frequency band, as opposed to spreading the same energy through a broader range of frequencies, may lead to an increase in amplitude, and consequently an increase in transmission distance (Morton 1975, Marten et al. 1977, Wiley and Richards 1982). The relatively long NFB notes also benefit from the calm air within a forest, leading to stability of attenuation characteristics and lower variability of signal degradation compared to more open habitat (Brown and Handford 1996, 2000). Interspecific acoustic convergence could also be affected by an interspecific function of the acoustic signal (e.g., Dobkin 1979, Baptista and Catchpole 1989). However, species-specific songs usually differ dramatically in frequency and temporal pattern of notes, which makes an explanation in the context of selection related to sound transmission more likely.

Another characteristic of NFB notes is that they probably lead to more difficulty for receivers to estimate the direction and distance of the sender (McGregor and Krebs 1984, Naguib 1996, Naguib et al. 2000). The lack of frequency modulation leads to a low potential for distance cues related to frequency-dependent attenuation (Shy and Morton 1986, Holland et al. 1998). Furthermore, long tails imply an omnidirectional nature of sound arrival, which may give the sound a ventriloqual character, similar to the

classic example of convergent alarm calls of small passerines to aerial predators (Marler 1959). Producing a loud signal for detection by conspecifics, which is at the same time difficult to locate for predators, may be another selection pressure that could drive song toward the use of NFB notes.

The beneficial consequences of reverberations associated with NFB notes are probably not restricted to dense tropical forests. Several studies have shown a strong impact of reverberations on signal degradation in temperate habitats (Dabelsteen et al. 1993, Mathevon et al. 1996, Holland et al. 1998). Therefore, reverberations may have played a role in the convergence of alerting introductory notes of many bird species found in North America (Richards 1981). Many introductory notes are typical NFB notes, and spectrograms clearly show evidence for reverberations extending their duration (e.g., Fig. 13 of Richards and Wiley 1982; Fig. 22.9 of Bradbury and Vehrencamp 1998), which supports the proposed function of these notes as alerting signals. Another intriguing comparison is the convergence to relatively high-pitched NFB notes in the song of many unrelated birds living close to fast-flowing rivers in the Himalaya (Martens and Geduldig 1989). Here, in the absence of dense vegetation, reverberations and the potential increase in effectiveness for NFB notes may be caused by atmospheric scattering in the constant turbulent air of this habitat.

Habitat-dependent transmission properties may lead to the convergence of song characteristics among species, but may also lead to divergence among populations within a species. Intraspecific divergence may develop if a species distribution covers multiple habitats in which transmission properties select for different acoustic designs. Many studies have shown habitat-dependent acoustic divergence among different populations of the same species (e.g., Anderson and Conner 1985, Handford and Lougheed 1991, Doutrelant and Lambrechts 2001), and a divergence in such a trait so closely linked to reproduction may be the initial step toward reproductive divergence and speciation (Slabbekoorn and Smith 2002). Measuring note slopes, as well as other more traditional acoustic measures, may be important for comparative studies addressing these evolutionary processes in the future.

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