

Acoustic Niches of Siberut Primates

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Abstract

The loud calls nonhuman primates use in long-distance communication have supposedly been selected for efficient information transfer in the habitat. The differential effects of scattering and reverberation and the masking effects of background noise predict that loud calls produced in rain forest habitats should be low-pitched and whistle-like with low-frequency modulation. Callers may also use particular calling posts or times of day with reduced background noise to increase the efficacy of sound transmission. We studied the loud calls of the 4 sympatric primate species on Siberut Island. Only Kloss gibbons (*Hylobates klossii*) fulfilled the predictions regarding both the structure and use of calls. Though the other 3 species – Mentawai macaques (*Macaca siberu*), pig-tailed langurs (*Simias concolor*), and Mentawai leaf monkeys (*Presbytis potenziani*) – also concentrated their main energies in the spectral window with the lowest background noise, their calls were not adapted to long-range transmission. All 4 species produced loud calls exclusively no lower than 18 m above ground, but food abundance and shelter in the canopy may also be factors. Though all 4 species produced the majority of loud calls in the morning, it was not the only time of day with reduced background noise. We suggest that phylogenetic inheritance may better explain the structure of calls than adaptation to the habitat. In sum, the observed usage of spectral and temporal niches is not solely an adaptation to the sound profile of the habitat, though it clearly improves their transmission.

Introduction

Most primates emit loud, conspicuous vocalizations termed loud calls or long-distance calls. Many of the loud calls that howlers, gibbons, langurs, and siamang emit, have acoustic characteristics that make them suitable for transmission over longer distances (Ryan and Kime 2003; Waser and Waser 1977). Therefore, individuals can use loud calls as intergroup signals over longer distances. Several researchers have explored the design of acoustic signals in relation to the individual's habitat (Brown et al. 1995; Forrest 1994; Nemeth et al. 2001; Padgham 2004; Waser and Brown 1984). They found that degradation of the spectral characteristics of acoustic signals and distortion of the temporal structure can occur. The degradation of acoustic signals leads to different structural changes, such as reverberations, irregular amplitude fluctuations and frequency-dependent attenuations (Bradbury and Vehrencamp 1998; Marten and Marler 1977; Marten et al. 1977; Naguib 1997; Wiley and Richards 1978). In general, they found that signals that concentrate energy in low frequencies propagate over larger distances than ones with high frequencies or those with energy spread over a larger frequency range. The same is true for the temporal domain. Fast trills with rapid frequency modulation transmit less well than slow trills (Naguib 2003). Therefore, in rain forests, loud calls should be low-pitched, whistle-like, and have a slow frequency modulation.

Spectral adaptation is not the only factor. Marten et al. (1977) found that sender height affects sound transmission more than most differences in habitat structure do and that the sound window of least-attenuated frequencies that Morton (1975) postulated occurred only close to the ground, <1m (Marten and Marler 1977). As a consequence, elevation to >1m above ground level during vocalization is the most effective way to increase effective range (Marten et al. 1977). Holland et al. (1998) and Padgham (2004) obtained similar findings, showing that position and height in the tree played a key role in the efficiency of call propagation. However, filtering and scattering of sounds alone do not determine the acoustic habitat; sounds other individuals in the same area emit are also a factor. In this way, species can improve the transmission of acoustic signals via a frequency range with reduced background noise or calling at a time when other individuals are silent.

Though researchers have explored how bird species occupy different acoustic niches within the same habitat (Naguib and Wiley 2001; Nemeth et al. 2006), information on how sympatric nonhuman primates use different spectral and temporal niches when communicating over long distances is sparse. We thus investigated the structure and use of loud calls of the 4 sympatric endemic primate species in primal rain forests on Siberut Island, Indonesia: Mentawai macaques (*Macaca siberu*), Mentawai leaf monkeys (*Simias concolor*), Mentawai langurs (*Presbytis potenziani*), and Kloss gibbons (*Hylobates klossii*). First, we recorded the loud calls of all 4 species and analyzed the extent to which the acoustic structure of their loud calls shows adaptations for an improved long-distance transmission. Second, we characterized the sound profile of the specific habitat and collected behavioral data on calling time and calling position.

Methods

Study Site and Subjects

We studied 4 native primate species on Siberut, the largest and most northerly of the Mentawai Islands. Siberut is 130 km off the west coast of Sumatra and is ca. 6700 km². Because the Mentawai archipelago has been isolated from the mainland of Sumatra for >500,000 yrs, much of its flora and fauna are unique. The study area is in the north of Siberut and is part of 4000 ha of primary rain forest under the protection of the Siberut Conservation Project (SCP). The study area has 13

radially placed transects with a mean length of 1.5 km (range 1–3 km; total 19.85 km; Waltert et al. in press) to facilitate behavioral observations. In 2005 a census of the SCP core study area indicated a primate denseness of 16 individuals/km² of Mentawai macaques; 8 individuals/km² of Mentawai langurs, 53 individuals/km² of Mentawai leaf monkeys, and 9 individuals/km² of Kloss gibbons in the study area (Waltert et al. in press).

Recording Loud Calls

During 3 mo from June to August 2005, we collected all-occurrences recordings *ad libitum* (Altmann 1986) between 0600 h and 1200 h and from 1300 h to 1800 h by walking along the transects. Before 0600 h, when it was still dark, we made additional recordings from the field station. In total, we had 324 observation hours. We recorded via a Sennheiser microphone (K6 power module, and ME66 recording head, and a MZW66 pro windscreen; Sennheiser Electronic KG, Germany) and a digital solid-state recorder (MARANTZ PMD660, Marantz, Japan). We recorded calls with a sampling rate of 44.1 kHz. In addition, we noted the time of the recordings, transect position, distance, and height of the caller. In total, we recorded 49 loud calls from Mentawai macaques, 116 loud calls from Mentawai langurs, 43 calls from Mentawai leaf monkeys, and 222 calls from Kloss gibbons (ca. 80% of the study area). We also noted transect position, distance, and height of the caller from loud calls when it was not possible to make a recording of the call.

We used the OPTI-LOGIC 100LH rangefinder (Opti-Logic, Tullahoma, TN) to estimate the height of the caller. Because of dense vegetation it was mostly impossible to make the necessary 3-point measurement with the rangefinder. Therefore, we established 4 height categories based on obvious vegetation differences (Fig. 1). With repeated measurements from the rangefinder, we calculated the height of the boundaries between the different height categories. We established the following 4 height categories (Fig. 1): zone 1, ground–1 m; zone 2, 1–18 m (transition from trunk to canopy); zone 3, 18–30 m (the top of the canopy); zone 4, >30 m ≤58 m (single standing large trees).

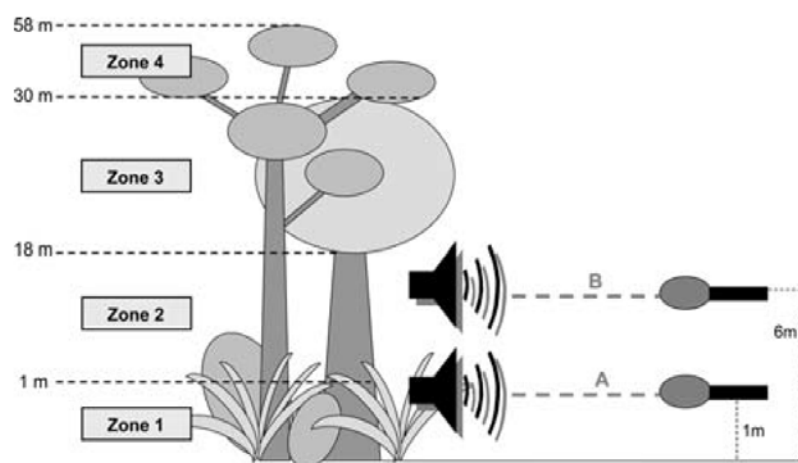


Fig. 1. Height categories and broadcasting conditions.

Acoustic Analysis

We inspected the loud calls and sampled ones that exhibited little disturbance by background noise via AVISOFT SASLAB Pro (R. Specht, Berlin). The loud calls of all 4 species comprised single elements, which one can onomatopoeically describe as barks, hoos, squeals, or trills. To distinguish between single call elements and whole loud calls we calculated the distribution of all silent intervals. The best time criterion to distinguish between single call elements and loud calls was 3 s. For a detailed acoustic analysis, we selected 7 high-quality recordings from Mentawai macaques, 9 from Mentawai langurs, 12 from Mentawai leaf monkeys, and 8 from Kloss gibbons. To increase the likelihood that the calls came indeed from different individuals, we used only calls that we recorded at different locations in the research area. We calculated a 1024-pt fast Fourier transform with a

frequency range of 8 kHz (frequency resolution: 15 Hz, temporal resolution: 64 ms). Based on the spectrogram, we calculated the following temporal parameters: call duration, number of elements per call, and the start/start interval of successive call elements. In addition, we described the energy distribution of the frequency spectrum. First, we calculated the logarithmic power spectrum of the calls via the same frequency/time resolution as above and estimated the peak frequency, the frequency with the highest amplitude in the power spectrum, with the bound cursor option (Avisoft SASLab Pro). To describe the range of the main energy, we measured the bandwidth of the peak frequency. We defined the main energy range by the lowest and highest frequency exceeding a threshold of 10 dB below the peak frequency. We chose the 10-dB threshold because lower thresholds could lead to an overlap with the background noise.

Background Noise

We measured the background noise (SPL (dB) re 20 μ PA) of the habitat via the sound level meter VOLTcraft 322 from Datalogger (Datalogger, Taiwan). This sound level meter has a frequency response range of 31.5–8000 Hz. We used the flat weighting scale (C). To track the daily course of the background noise we measured the sound pressure levels from dawn (0700 h) until dusk (1800 h). In addition, we performed 1 measurement before sunrise at 0600 h and 1 after sunset at 1900 h. We also took 3 measurements in the night between 2100 and 2300 h and during rainfall. We conducted the nocturnal measurements at the field station.

To consider differences in habitat structure we measured the background noise at 2 different sites: Site 1 has medium-rise plant cover on the ground. It was a marshy area in which rainfall formed little ponds in which frogs immediately settled. Site 2 was an area with large trees and low ground cover, but with several small patches of bamboo. We measured at each site in 4 directions (0°, 90°, 180°, and 270°). For each direction we took a 90-s measurement of the minimum and maximum sound pressure level. We performed all measurements during the day, 3 times at each place. We also measured the sound pressure level during rainfall and shortly after rainfall. We also made acoustic recordings of the different background noise conditions and analyzed them the same way as the recordings of the loud calls. We tested the differences in circadian sound level via a Mann-Whitney U-Test (SPSS 12, SPSS Inc., Chicago, IL).

Results

Description of Loud Calls

Male Mentawai macaque loud calls are made up of rough barks, which can vary in number of elements and repetition rate (Table 1). Usually, their loud calls start with a fast repetition rate that decreases toward the end of the call (Fig. 2). The main energy of their loud calls is concentrated between 0.9 and 1.2 kHz, which is similar to the main frequency range of Kloss gibbons (Table 1).

Mentawai leaf monkeys and Mentawai langurs showed a broader peak bandwidth, and leaf monkeys had the highest frequencies (Table 1; Fig. 2). The loud calls of the Mentawai leaf monkeys comprised barks and squeals. The barks were clearly louder than the squeals that seem to be produced by inhalation. In leaf monkeys, the repetition rate of the elements was often lower than that of the loud calls of macaques or Mentawai langurs (Table 1).

The loud calls of Mentawai langurs comprise barks and hoos. The barks are noisy calls similar to macaque barks. The hoos sound similar to the hoos of Kloss gibbons, though they differ clearly in their peak amplitude (Table 1). Typical Mentawai langur loud calls begin with barks and end with hoo elements.

Table 1. Time and frequency characteristics of loud calls

Call characteristics	Mentawai macaques	Mentawai leaf monkeys	Mentawai langurs	Kloss gibbons
Call duration (s)	4.6 ± 1.7	20 ± 14	5.2 ± 0.9	26 ± 13
Number of elements	B: 6 ± 3	B: 13 ± 14 S: 6 ± 3	B: 7 ± 2 H: 5 ± 1	T: 34 ± 21 H: 6 ± 2
Start/start interval (ms)	300-500	300-1000	200-500	150-3000
Peak frequency (Hz)	B: 1058 ± 166	B: 1481 ± 182	B: 1184 ± 386 H: 482 ± 29	T: 975 ± 102 H: 1010 ± 15
Bandwidth of main energy (Hz)	932 ± 107	1250 ± 165	940 ± 307	881 ± 86
	- 1199 ± 272	- 1748 ± 125	- 1788 ± 605	- 1084 ± 106

Shown are means ± SD. B = barks; S = squeals; H = hoos; T = trills.

The loud calls of Kloss gibbons differ clearly from the loud calls of the other 3 species (Fig. 2); they had a tonal structure throughout. A typical Kloss gibbon loud call started with some slowly repeated hoos, which pass into trills with a higher repetition rate. The end of the loud call again could be made up of hoos with a lower repetition rate. The number of trills was variable (Table 1).

Though the loud calls of Mentawai macaques, Mentawai leaf monkeys, and Mentawai langurs consisted mainly of bark-like elements, it was not difficult to distinguish between them. The combination between repetition rate and main frequency energy give them a species-specific sound characteristic. Together with the additional elements, squeals in Mentawai leaf monkeys, hoos in Mentawai langurs, and only barks in Mentawai macaques, the loud calls have a clear species specificity.

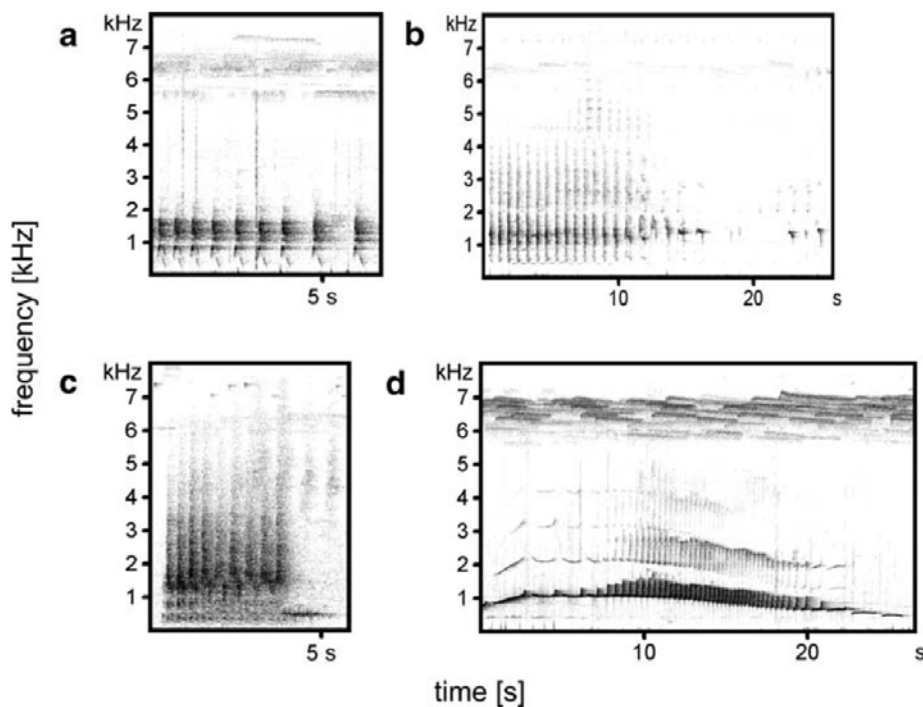


Fig. 2. Spectrograms of typical loud calls. (a) Mentawai macaque (*Macaca siberu*). (b) Mentawai leaf monkey (*Simias concolor*). (c) Mentawai langur (*Presbytis potenziani*). (d) Kloss gibbon (*Hylobates klossii*).

Circadian Distribution of Loud Calls

All 4 species emitted the majority of their loud calls in the morning (Fig. 3). Mentawai macaques produced their largest number of loud calls between 0700 and 0800 h with a second peak between 0800 and 0900 h. The distribution of loud calls of Mentawai leaf monkeys had no clear peak. Though they produced most of their calls 1 h earlier, between 0600 and 0700 h, the differences in the morning hours (0800–1000 h) were small. In contrast to leaf monkeys, Mentawai langurs had 1 prominent peak between 0600 and 0700 h. Kloss gibbons had a bimodal distribution in their morning calling, 1 between 0500 and 0600 h and 1 between 0800 and 1000 h. With the exception of Kloss gibbons, the 3 other species slightly increased their vocal activity in the afternoon. Kloss gibbons were also the only species that called in the night. Though all species preferred the morning hours, their vocal activities did not overlap.

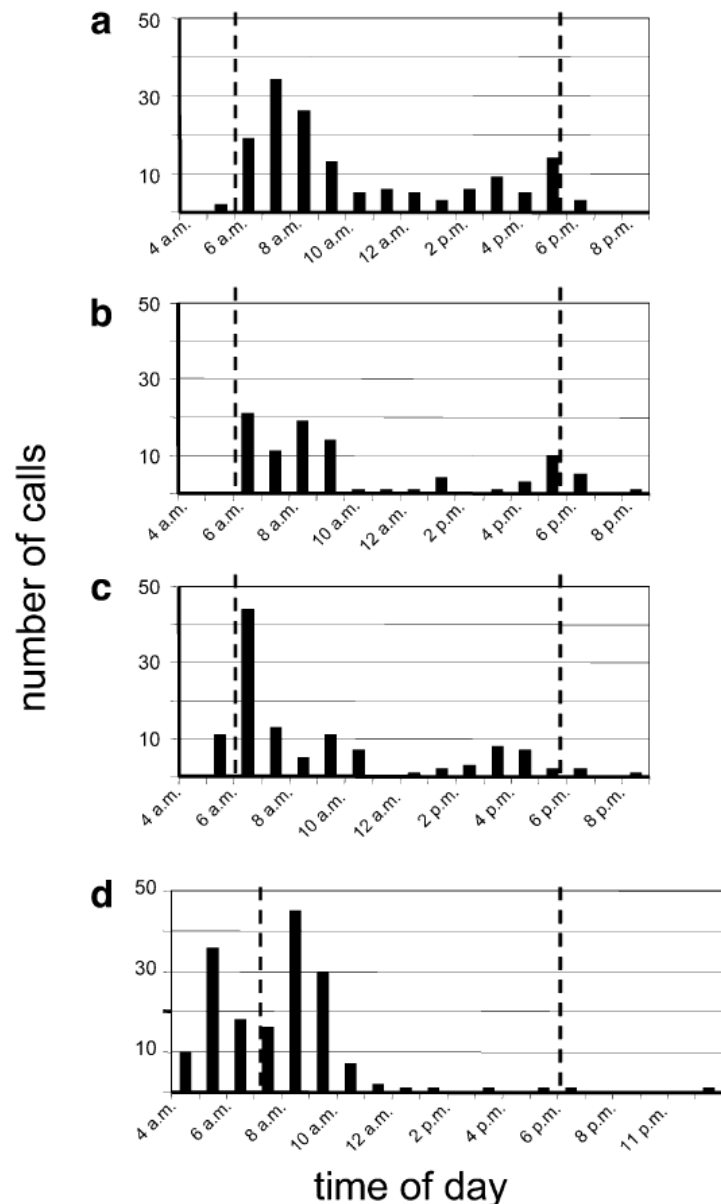


Fig. 3. Circadian distribution of loud calls. (a) Mentawai macaque (*Macaca siberu*). (b) Mentawai leaf monkey (*Simias concolor*). (c) Mentawai langur (*Presbytis potenziani*). (d) Kloss gibbon (*Hylobates klossii*). Dashed lines = sunrise and sunset.

Background Noise

Figure 4 contains 2 spectrographic examples characterizing the background noise in the Peleonan Forest. Insects were the main source of constant background noise (Fig. 4). Power spectra calculations of recorded background noise showed main peaks at ca. 6 kHz (mean: 5972 Hz \pm 460 Hz SD). Frogs and birds were additional sources of noise, but much more scattered in time and space. The main energy of frog sounds was clearly above the frequency energy of the loud calls of all 4 primate species (frogs: mean 2699 Hz \pm 501 Hz SD). The main energy of bird sounds depended mainly on the species. The recordings in Fig. 4 show a frequency range similar to that of frogs or below the main energy of the loud calls of the primates. Nevertheless, some bird species also sang or called within a similar frequency range.

Sound level measurements revealed relatively constant values during the day with an increase during the evening (Fig. 5). At site 1 the mean maximum values increased from 55 dB at 1500 h to 63 dB at 1700 h and 72 dB at 1900 h. Similarly at site 2, the mean maximum values increased from 47 dB at 1600 h to 64 dB at 1800 h or to 69 dB at 1900 h. In both places the lowest background noise occurred in the afternoon between 1400 and 1600 h. Accordingly, there is no significant difference in the background noise level between morning and afternoon (site 1: $U=20$, $p=0.684$; site 2: $U=19$; $p=0.599$), but significant differences between morning and evening (site 1: $U=-6$; $P=.03$; site 2: $U=0$; $p=.001$).

Raindrops from the vegetation led to a sound pressure level between 46 dB and 58 dB. Rainfall itself resulted in sound pressure levels between 59 and 66 dB. In both cases, rainfall during the morning, noon, and afternoon could lead to an increase of background noise, whereas during the evening, rainfall did not cause an increase of the amplitude of background noise. In contrast to other sources of background noise, rainfall produces wideband random noise (Fig. 5).

Calling Height and Sound Propagation

All 4 species produced loud calls exclusively in the 2 top zones, 18–58 m above the ground (Fig. 1). Whereas Mentawai macaques, Mentawai leaf monkeys, and Mentawai langurs used zones 3 and 4, Kloss gibbons preferred to sing in zone 4. Though all 4 species sometimes descended to emit other call types, Mentawai macaques were the only ones that vocalized while on the ground (alarm calls).

To examine frequency-dependent propagation characteristics, we broadcast and rerecorded different sine tones. At a distance of ≤ 50 m at a height of 1 m and 65 m at a height of 6 m there is no significant difference in frequency-dependent attenuation of the sine tones. At 100 m we obtained no usable rerecording

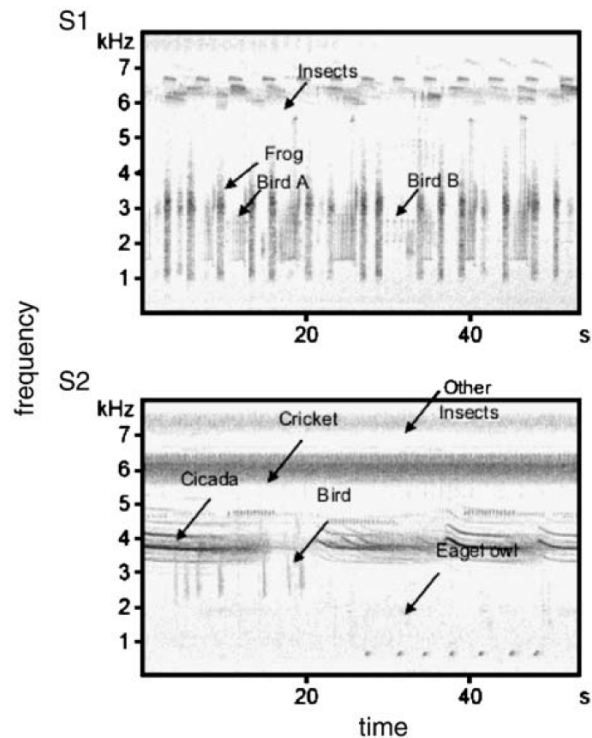


Fig. 4. Spectrogram of background noise at sites 1 (S1) and 2 (S2).

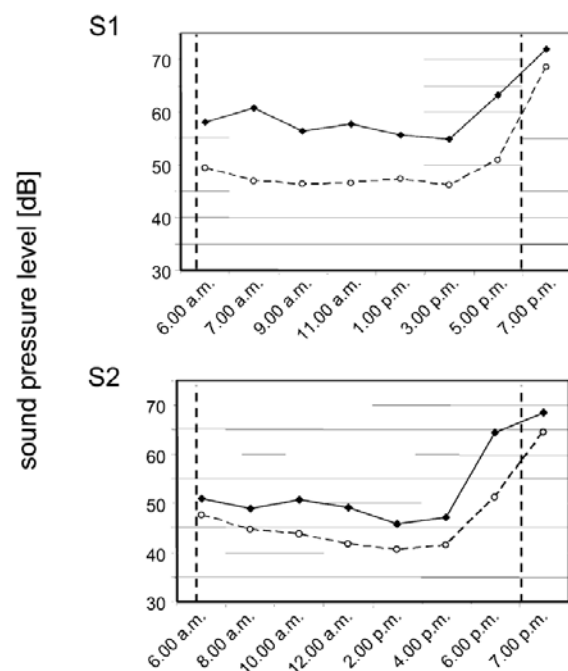


Fig. 5. Minimum and maximum sound pressure levels of the background noise at sites 1 (S1) and 2 (S2). Squares with dotted line = minimum sound pressure; circles with solid line = maximum sound pressure. Dashed lines = sunrise and sunset.

Discussion

Only Kloss gibbons showed clear adaptation for improved long-distance transmission in the spectral structure of their loud calls. The energy of their loud calls was concentrated in a single-frequency band, with a low peak frequency in relation to body size and a low-frequency modulation of call elements. All 4 species concentrated the main energy of their loud calls outside the frequency range of insect sounds, the main source of constant background noise. All 4 primate species produced the majority of their loud calls during the morning, when background noise was reduced versus that in the evening. In addition, all 4 species produced their loud calls exclusively in the 2 top vertical zones, 18–58 m above the ground.

Structural Adaptation for Long-Distance Communications

The distance at which a signal is transmitted efficiently depends on the energy of the source and the distortion during propagation (Forrest 1994; Martens and Michelsen 1981; Padgham 2004; Price et al. 1988). Several researchers who have explored the design of acoustic signals in relation to habitat have found that signals with low frequencies and energy concentrated in a small frequency band propagate over larger distances than signals with high frequencies or wideband signals with distributed frequencies (Brenowitz 1986, Brown et al. 1995; Brown and Gomez 1992, Forrest 1994; Nemeth et al. 2001; Waser and Brown 1984, 1986). Studies on birds (Padgham 2004) and with artificial sounds (Nemeth et al. 2006) have revealed that in rain forest habitats, narrow-band signals, with slow-frequency modulation, and a frequency range between 1 and 3 kHz travel best.

Accordingly, loud calls produced in rain forest habitats should be low-pitched, whistle-like, with a slow amplitude or frequency modulation. The loud calls of Kloss gibbons fulfil these criteria. With the exception of the soft hoo elements at the end of the loud calls of Mentawai langurs, the loud calls of the other 3 species show no sign of such adaptation. The soft hoo elements in the loud calls of Mentawai langurs have some similarities with the hoos of gibbons, but their sound level did not exceed half of the sound level of their bark elements. It remains unclear whether the soft hoo elements are loud enough to serve as energy-saving elongation of their loud calls. Mentawai macaques and Mentawai leaf monkeys showed no adaptation in the frequency structure of their loud calls.

Calling Location

Marten et al. (1977) found that sender height and frequency affect sound transmission more than habitat does. More recent studies (Holland et al. 1998; Nemeth et al. 2006; Padgham 2004) suggest that height in the tree while calling plays a key role in propagation efficiency. We found a good adaptation in all 4 species because subjects emitted no loud calls lower than 18 m above ground. However, the extent to which other social or ecological factors might have influenced the finding is unclear, though for macaques at least we observed numerous activities, including other vocal utterances, on the ground.

Background Noise

Background noise also defines the sound profile of a habitat. Like other rain forest habitats (Brown and Waser 1988; Waser and Brown 1986), the background noise in Siberut derived mainly from insects, frogs, and birds. The main energy of frog sounds lies above the main energy of the loud calls of the 4 primate species. In addition, in Siberut, frogs live mainly near the ground; therefore, though their calling can reach high sound levels, it did not overlap much with the loud calls of the primates. Birds are more dispersed in the habitat but their songs are shorter and more discontinuous

than the sounds of frogs and insects. Though many birds sing or call outside the main frequency range of the primate loud calls, some sing or call within the same frequency range. Insects are the critical source of background noise because they make mainly continuous sounds and are widespread over all locales and heights in the habitat. We show that the main energy of the loud calls of the primate species was outside the frequency range of insect sounds.

Calling Time

The 4 primates produced the majority of their loud calls during the morning, when the level of background noise was reduced versus that in the evening. Because the background noise was also low at noon and early afternoon, one cannot explain the time window for calling exclusively in terms of the sound pressure of the background noise. Henwood and Fabrick (1979) and Waser and Waser (1977) argued that that thermal gradients make sound transmission more efficient in the morning. Irrespective of whether the thermal gradient argument applies to different height and canopy compositions, only Kloss gibbons called very early in the morning or at night. The 3 other species did not use the early morning hours exclusively, but also called until late in the morning. There are further explanations why the primates call in the morning but not in the afternoon or at dusk. Brown und Gomez (1992) focused on social context for a dawn chorus. Another argument not to call late in the afternoon or at dusk is the safety of lodge trees because primates leave them in the morning and usually choose different trees the next evening.

Summary

In sum, only gibbons utter loud calls that fit the predictions of sound transmission principles. The loud calls of the other 3 species showed only partial adaptations regarding the requirements of long-distance communication. Perhaps this is not so surprising because loud calls are not solely used for intergroup communication. Loud calls are emitted in a variety of circumstances and can serve different functions, such as defending or attracting mates or to maintain contact (Cheney et al. 1996; Steenbeek et al. 1999, Tenaza 1989; Waser 1977; Wich and Nunn 2002; Wich et al. 2002). For instance, in rain forests individuals can use loud calls to locate group members that are nearby but outside visual contact. An optimized sender locating can be more important than a signal that can travel over longer distances.

It remains difficult to answer to what extent the main frequency range of the loud calls is a consequence of the existing frequency niche. Loud calls are relatively stereotyped vocalizations (Ryan and Kime 2003) with strong phylogenetic roots (Wich and Nunn 2002). Many primate species emit bark-like loud calls, independent of whether they live in rain forest or savanna habitats. Except for the gibbons, the other 3 species showed a relationship between body size and main frequency of their loud calls that follows the general rule that smaller primates produce loud calls with higher frequencies (Ey et al. 2007a, b). Together the findings suggest that the frequency niche was not the only selective force for the actual main energy level of the bark-like loud calls of the 3 species.

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