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The Ecology of Singing in Kloss Gibbons *(Hylobates klossii)* on Siberut Island, Indonesia

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Data are presented from a study of habituated Kloss gibbons on Siberut Island, Indonesia. Male Kloss gibbons can sing at any time from 0100 to 1300 hr, but the majority of songs is concentrated in the hour before dawn. Female Kloss gibbons sing only after dawn and the song bout includes a dramatic visual display. Neither countersinging nor coordinated chorusing has been proved in either sex. Males sing before dawn as often as possible but are inhibited by wet nights and by minimum temperatures below 21.5°C; postdawn songs of both sexes are inhibited by rain. The occurrence of any particular type of song bout is independent of the occurrence of the other types. Song trees used by males and those used by females do not differ in height. Song trees emerged from the neighboring canopy more than other available trees of similar height in the gibbons' home range. Female song trees were most abundant on the slopes and where the trees were tallest. Almost all the male's night trees could have been used for singing from had the weather been suitable. There was a greater likelihood of the male's traveling a long way to the day's first fruit source on mornings when he sang before dawn than on mornings when he did not. Considerations of sound transmission through tropical rain forest reveal that the times and frequencies used for singing by Kloss gibbons are optimal for communicating with neighboring groups.

KEY WORDS: gibbons; Siberut; ecology; singing; environmental effects.

INTRODUCTION

Gibbons (Primates: Hylobatidae) are monogamous, territorial apes that inhabit the rain forests of Southeast Asia. Both sexes sing loud, sex-specific songs

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of varying complexity (Marshall and Marshall, 1976). The likely functions of the male song may be summarized as defense and advertisement of his territory, and mate attraction, and the likely function of the female song as a declaration that the male is already paired (Gittins, 1978, 1979; Whitten, 1980, 1982a).

Vocal duets by the adult pair are characteristic of monogamous animals (Diamond and Terborgh, 1968; Lamprecht, 1970; Wilson, 1975) and it has been suggested that duets serve to maintain the pair bond (Thorpe and North, 1965, 1966; Hooker and Hooker, 1969; Thorpe, 1961; Chivers, 1974). Duetting has been confirmed for all species of Old World primates that are known to live only in monogamous groups [spectral tarsier *Tarsius spectrum* Pallas (MacKinnon, 1981); indri *Indri indri* Gemlin (Pollock, 1975); Mentawai langur *Presbytis potenziani* Bonaparte (Tilson and Tenaza, 1976); gibbons (Marshall and Marshall, 1976)] with the exception of Kloss gibbons *Hylobates klossii* Miller, in which the sexes sing independently of each other. The lack of a duet is probably a derived rather than a primitive feature (Haimoff *et al.*, 1982) and should be viewed as one extreme of a spectrum of gibbon vocal interactions, the other extreme being represented by the siamang *H. syndactylus* (Raffles), in which the male and female sing highly structured duets (Haimoff, 1981).

In other detailed field studies of gibbons in which the analyses of singing behavior played a significant role (Chivers, 1974; Tenaza, 1976; Gittins, 1978, 1979), no great attempt was made to determine how singing related to the gibbons' environment.

In this paper an attempt is made to redress these omissions using data from habituated Kloss gibbons on Siberut Island, Indonesia. The majority of the data was collected from a single group, but observations of other groups did not contradict any of the findings.

METHODS

For about 2 years between 1976 and 1978 Kloss gibbons were studied on Siberut Island, the largest and most northerly of the four Mentawai Islands, which lie 85–135 km off the coast of West Sumatra, Indonesia. The study area comprised 200 ha of hilly lowland evergreen rain forest above the Paitan River in central Siberut at 1°21'S, 98°59'E (Fig. 1). A group of three gibbons (BG4) was habituated to an observer and studied intensively from May 1977 until the male was shot by a local hunter 6 months later. During that period the adult female died, and a second, initially unhabituated, female entered the home range 2 weeks later (see Whitten, 1982a). Nearly 500 hr of close observations of this group was achieved, including 22 days of following BG4 between consecutive night trees. (A night tree is the tree entered in the late afternoon in which the gibbons sleep until the following dawn.) After the male's death, the adult female

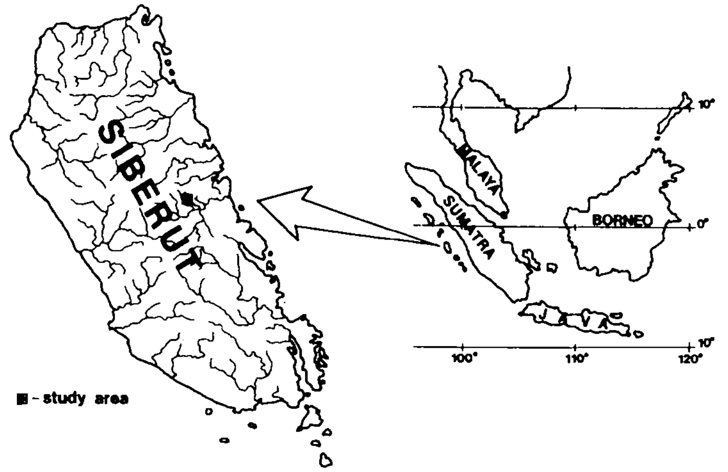

Fig. 1. The location of the study area on Siberut Island, and its location in Southeast Asia.

and juvenile dispersed and another group of three members (BG10) entered the vacated home range from the northeast of the study area.

For each night tree and song tree, the identification, total height, abundance of vines and epiphytes (*Myrmecodia tuberosa* Jack) on a scale of 0–3, and position of the crown relative to the neighboring canopy were recorded. These and other variables were also recorded for 2459 trees of at least 15-cm diameter at breast height along 20-m-wide transects (total, 11.25 ha) and were used in an analysis of vegetation composition and structure (Whitten, 1980, 1982c). This resulted in different forest types' being identified, making it possible to estimate the number, species, and structure of trees in BG4's home range (Whitten, 1980, 1982d).

In addition to using detailed check-sheets, a shorthand summary of events was kept on each day that gibbons were followed. These included the time of onset, duration, and location of all songs, and the location of the gibbons. This was monitored continuously with reference to a mapped grid system, known food trees, and rivers. Locations were usually accurate to within 10 m. The presence and absence of songs given by BG4 were recorded accurately over 89 days between April and October 1977. The data on the frequency of singing and the majority of statistical analyses are confined to this period.

The start of a gibbon day is related to the time of dawn (Chivers, 1974; Gittins, 1979; Whitten, 1980). All times relating to gibbons were recalculated from West Indonesian time to "time after dawn," which was taken as 0600 hr.

Gibbon songs were tape-recorded on a Uher 4000 Report-L lent to me by Dr. David Chivers. The songs are represented by sonagrams (plots of all frequencies against time) which have been traced omitting extraneous noises such as machine hums, echoes, and cicada and bird calls. The sonagrams were produced on a Kay Sonagraph 6061B sound spectrograph operated by Mrs. Joan Hall-Craggs at the Sub-department of Animal Behaviour, University of Cambridge.

Rainfall, maximum and minimum temperatures, and whether it had rained between the previous dusk and dawn were recorded at 1700 hr on each day spent in the study area. The weather conditions were recorded as one of a series of seven mutually exclusive classes every 10 min from dawn to dusk on the days gibbons were studied intensively.

Normally distributed data were taken as those having indices of kurtosis and skewness whose sum did not exceed 1.00. Few data met this criterion, and so most analyses required nonparametric statistics. Unless indicated otherwise, the symbols and statistical tests used in this paper may be found in Siegel (1956). Correlations are tested with a one-tailed region of rejection; all other tests are two-tailed.

RESULTS

Male Songs

The songs of male Kloss gibbons have been described in detail elsewhere (Tenaza, 1976; Whitten, 1980, 1982b). Songs start with simple, single notes (±0.7 kHz), progressing gradually to elaborate trilling phrases (0.6–1.0 kHz) (Fig. 2), which can be heard from 1.5 km away and may be given before dawn from a night tree or after dawn. The BG4 male sang before dawn every 2.0 days,

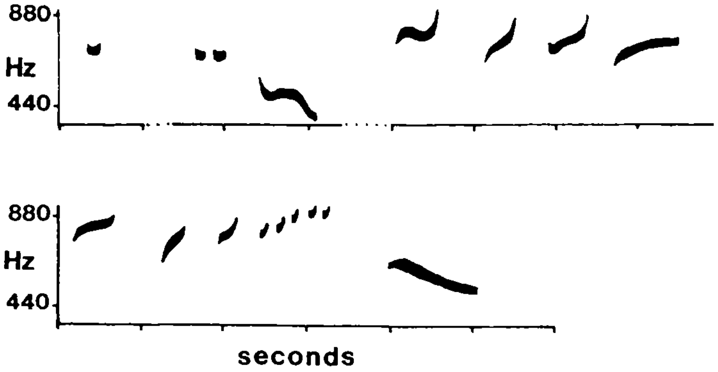

Fig. 2. Progressive stages in the male song.

after dawn every 9.8 days, and overall every 1.7 days. The median length of songs is 44 min (range, 3–108 min).

It is common for males to sing at more or less the same time. Tenaza (1976) suggests that this involves countersinging [sensu (Armstrong, 1963): "non-random vocal interactions between neighbors of the same sex"], but no data have been collected from any gibbon species to suggest that the term may be used unequivocably. These "choruses" are not coordinated activities; in a sample of 55 days on which some singing was heard before dawn, the BG4 male sang alone on 3 days and remained silent while others sang on 11 further days. It is certain, however, that singing by one gibbon can act as a releasing stimulus (Tinbergen, 1951; Hinde, 1970) to another if it is sufficiently motivated (Gittins, 1978).

Predawn songs sometimes started as early as 0100 hr. The modal time class was 0500–0515 hr, during which 20% of the predawn songs began. Most predawn songs stopped at dawn or soon after (Fig. 3). Exact times were difficult to obtain

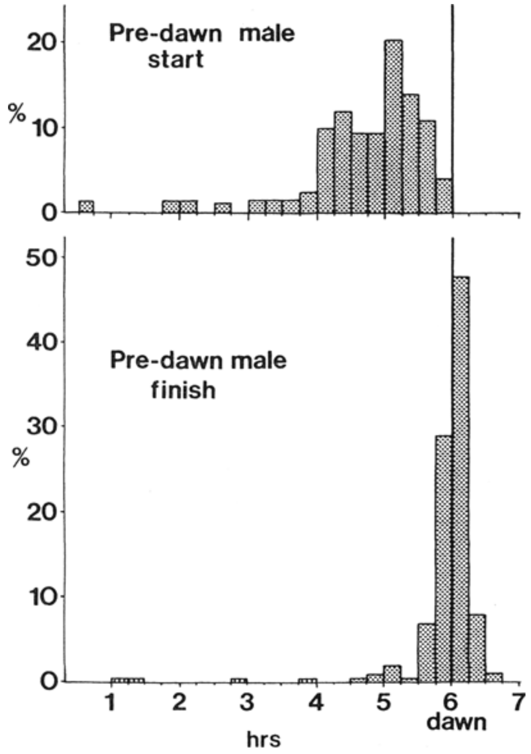

Fig. 3. Distribution of the start of the first, and the finish of the last, predawn male song heard each day during 1977 in 0.25-hr periods through the day (N = 233).

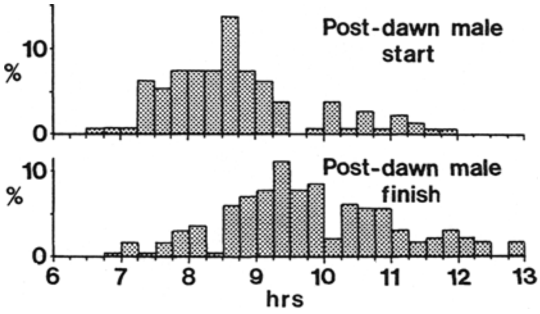

Fig. 4. Distribution of the start of the first, and the finish of the last, postdawn male song heard each day during 1977 in 0.25-hr periods through the day ($N = 83$).

on some occasions because of the deafening chorus of cicadas, but this had usually abated by 0610 hr. Postdawn male songs could begin at 0700 hr, after the first major feeding bout of the day, and the latest started just before 1200 hr (Fig. 4).

Female Songs

The song of female Kloss gibbons has been described as "probably the finest music made by any wild land mammal" (Marshall and Marshall, 1976) and is analyzed in detail elsewhere (Tenaza, 1976; Whitten, 1980). The song is preceded by about 3 min of essentially single-pitched (0.7-kHz) notes. Each part (termed here a "great call") of the song itself lasts about 30 sec and comprises a series of rising notes (0.6–1.0 kHz), a trill (1.0–1.2 kHz), and falling notes (1.0–0.4 kHz). Song bouts incorporate a dramatic visual display, as do the female songs of lar gibbons, siamang (Chivers, 1974), and agile gibbons, *H. agilis* Cuvier (Gittins, 1979), during which the female leaps through the forest canopy, twisting and turning, and tearing leaves from branches.

A song bout comprises, on average, about 20 great calls and lasts about 20 min. The first BG4 female sang 12 times in 43 days (once every 3.6 days), whereas the younger, second BG4 female sang 6 times in 33 days (once every 5.5 days).

Tenaza (1976) reported that neighboring adult female Kloss gibbons engaged in bouts of "countersinging" by singing in unison across a shared territory boundary. Unison singing between adult females has not been reported in other field studies of gibbons, but all, except Tenaza (1976), report mothers and juveniles singing together [lar gibbon (Carpenter, 1940); siamang (Chivers, 1974); pileated gibbon, *H. pileatus* Gray (Marshall and Marshall, 1976); agile gibbon (Gittins,

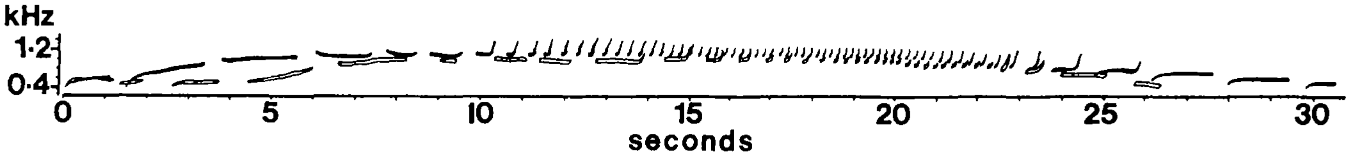

Fig. 5. Great call given by adult female (filled shapes) and her juvenile offspring (open shapes).

1979); Mueller's gibbon, *H. muelleri* Martin (D. Leighton, personal communication)]. During this study, 13 adult females were observed singing on a total of 35 occasions. On none of these, however, were adult females seen to sing in unison, although mothers and juveniles were frequently seen to sing together (the 35 occasions) (Fig. 5). Simultaneous singing with a neighbor has been found to be disadvantageous in birds (Wasserman, 1977). Tenaza may have misinterpreted his observations of unhabituated Kloss gibbons, which, being totally black and with few individual features (Groves, 1972; Whitten, 1980), are extremely hard to tell apart.

The modal time class for the start of female songs was earlier than that for postdawn male songs (Fig. 6), but a median test on their combined median (0833 hr) revealed no significant difference ($\chi^2 = 2.2$, df $= 1$, $P > 0.05$).

The first BG4 female sang alone on 1 of the 19 days on which at least one female song was heard during a 3-month sample. On a further 7 of these 19 days, at least one of the females surrounding the BG4 female sang, but she remained silent. The absence of perfectly coordinated chorusing in female songs is probably also explicable in terms of variable and uncoordinated motivation.

Environmental Influences

I gained the impression in the field that singing before dawn was less common after wet nights. Of 370 early mornings at the study area, spent either in the forest or in the adjacent camp listening for male songs, rain fell between 2100 and 0600 hr on 100 days (27%). Males sang before dawn on 254 days (68%), yet during 85% of those nights no rain fell. There was a highly significant

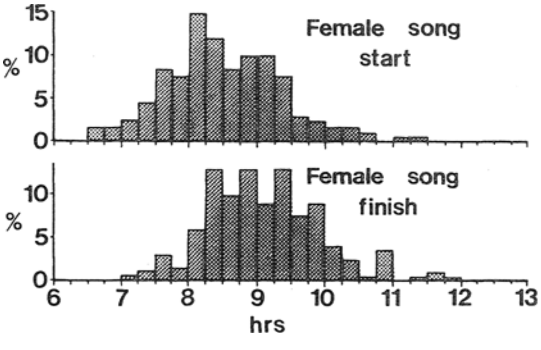

Fig. 6. Distribution of the start of the first, and the finish of the last, female song heard each day during 1977 in 0.25-hr periods through the day ($N = 183$).

relationship between rain in the night and the absence of singing before dawn ($\chi^2 = 59.65$, df $= 1$, $P < 0.001$).

Rain fell between 2100 and 0600 hr on 20 of the 89 days between April and October 1977 on which it is known whether or not BG4 sang, and on none of those days did the BG4 male or the seven other males audible from his home range sing before dawn. There were, however, 14 other days within that sample on which no rain fell during the night but on which no singing before dawn was heard.

The minimum temperature was reached in the hour before dawn when most songs began. The temperature the gibbons experienced and the temperature in the camp where the temperature was recorded were probably different, but the differences were considered relatively constant. A Mann–Whitney U test on the 69 "dry nights" from the 89-day sample revealed that the minimum temperature on days when no singing was heard before dawn was significantly lower than that on days when singing was heard ($z = 3.59$, $n_1 = 14$, $n_2 = 55$, $P < 0.001$). The median minimum temperature for dry nights on which singing was heard before dawn was 22°C, and that for dry nights with no songs was 21.5°C.

The huddled position of sleeping gibbons—limbs close to the body and head resting on the knees—is an excellent position for conserving body heat. Singing required the head to be held up, thereby exposing the sparsely haired neck and chest, and it would seem that the colder it is just before dawn, the less likely the male is to sing and thus lose heat.

Postdawn song bouts of male and female never occurred during rain, and this has been observed for other gibbon species (Chivers, 1974; Gittins, 1979). Postdawn songs occurred too infrequently to allow statistical analyses of environmental influences to be performed.

Interdependence of Songs

Four major classes of song bouts were distinguished:

(1) predawn male songs;
(2) postdawn male songs (before female songs or if female songs did not occur);
(3) female songs; and
(4) postdawn male songs (after female songs).

The probabilities of each type of song occurring on any day were 0.49, 0.15, 0.27, and 0.08, respectively.

Eleven daily combinations of these classes of song bouts were recorded for BG4 during the 76 days of the 89-day sample in which the group included an

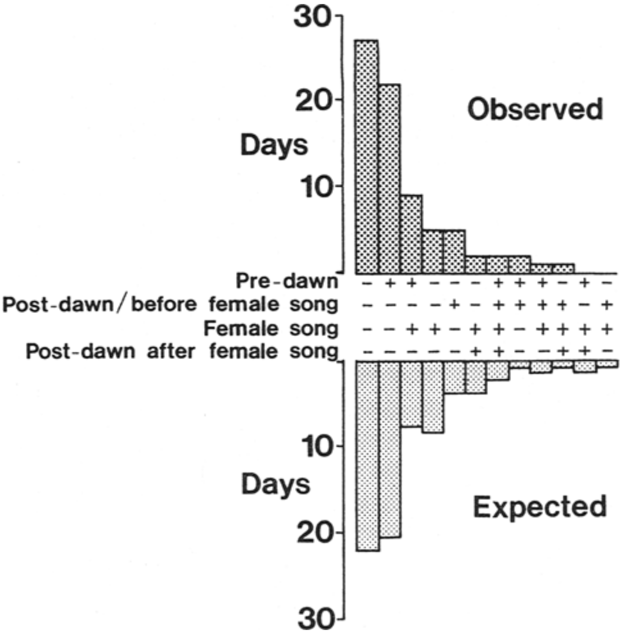

Fig. 7. The observed and expected number of days of 76 on which different combinations of songs were given by BG4. (+) "given"; (–) "not given."

adult female. It is possible that female songs were given only if the male had sung before dawn, or maybe it was necessary for males to sing after dawn before the female would sing. To investigate these possibilities, the probability of each combination's occurring was calculated, assuming no dependence among the different classes of song bouts. For example, the probability of the male's singing before dawn and of the female's singing on one day is $0.49 \times (1 - 0.15) \times 0.27 \times (1 - 0.08) = 0.10$. The observed and expected frequencies are compared in Fig. 7, and no significant difference was found ($\chi^2 = 3.23$, df = 4, $P > 0.05$). This suggests that the occurrence of each class of song bout was independent of the occurrence of the others.

Song Trees

Thirty song trees were located within the home range of BG4. The majority (70%) was species of *Dipterocarpus;* only three supported vines from which the gibbons had eaten, and two were potential food sources themselves.

Structure

The median height of song trees used by the BG4 females was 42 m, and the median height of song trees used by the BG4 male was 37 m, but a median test revealed no significant difference ($\chi^2 = 1.15$, df = 1, $P > 0.05$). The frequency of song trees with and without vines did not differ significantly from that found for the population of "tall trees" (>34 m) estimated to be in the home range (see Whitten, 1982d) ($\chi^2 = 0.46$, df = 1, $P < 0.05$). Similarly, the frequency of song trees bearing *Myrmecodia tuberosa* epiphytes did not differ from the expected ($\chi^2 = 0.36$, df = 1, $P > 0.05$). It appears, however, that there were significantly more song trees with an exposed crown (50%) and fewer in the other classes (50%) than expected (27 and 73%, respectively) ($\chi^2 = 7.03$, df = 1, $P < 0.01$).

Song trees were, therefore, typically more emergent than other trees of the same or similar height, presumably to allow the song to be heard and the females' acrobatic display to be seen at the maximum possible distance. There is no evidence that the presence of biting ants from the myrmecophilous *Myrmecodia* affected the choice of song trees as there is for the choice of night trees (Whitten, 1982e). This is probably because singing is a more active and a much shorter activity than sleeping.

Distribution

The distribution of song trees in relation to the home range and territory of BG4 (Whitten, 1982d) is shown in Fig. 8. The distribution of male and female song trees used after dawn between the two areas did not deviate significantly from the expected distribution based on area ($\chi^2 = 2.17$ and 1.02 for male and female song trees, respectively; df = 1, $P > 0.05$, in both cases), although the majority of the male's trees was very near the territory boundary.

Although the BG4 male sang before dawn every second day on average, he sang on 37 (70%) of the 51 occasions on which his night tree was located, a discrepancy caused by the relative ease of finding him when he sang. None of the six trees that were recorded as night trees on three or more occasions was used exclusively for singing or for remaining silent.

If each of the 51 occasions on which the male was found before dawn is regarded as a separate event in a separate tree, the heights of night trees used for singing were not significantly greater than those of night trees where he remained silent (median test: $\chi^2 = 0.08$, df = 1, $P > 0.05$). It is likely, therefore, that the majority of night trees would be suitable for singing from before dawn, and whether or not the male song was probably determined primarily by the weather.

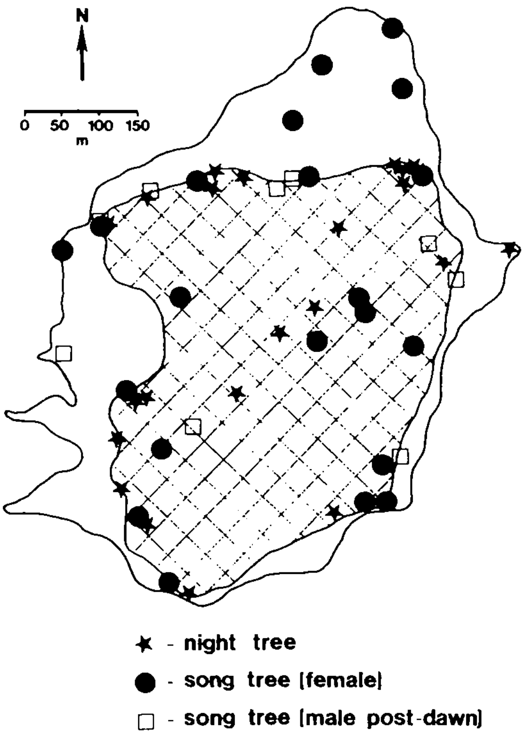

Fig. 8. The home range and territory (cross-hatched) of BG4 with the location of night trees, female song trees, and postdawn male song trees.

It has been suggested that small gibbons in hilly terrain might tend to use tall trees on slopes for sleeping because the male sings before or at dawn (Gittins, 1979). If they slept in the flatter areas, the range of the songs would be reduced because any intervening hills would cause sound shadows. Had this been true for the BG4 male, he would have been expected to sing most often from the higher elevations in his home range. In fact, although there were significantly more night trees on the slopes, there was no more significant difference between the frequency of singing in flat areas (14 nights) and the frequency of singing on slopes (37 nights) than expected from the frequency of night trees in the two areas (Whitten, 1980). Thus, he was not inhibited from singing when in the flat areas, and the position of the home range in the study area, as shown in Fig. 9, provides a clue why this should be so.

The high ridge (± 150 m) to the north represents a major barrier to sound, and the BG4 male probably heard fewer songs from that direction than from the

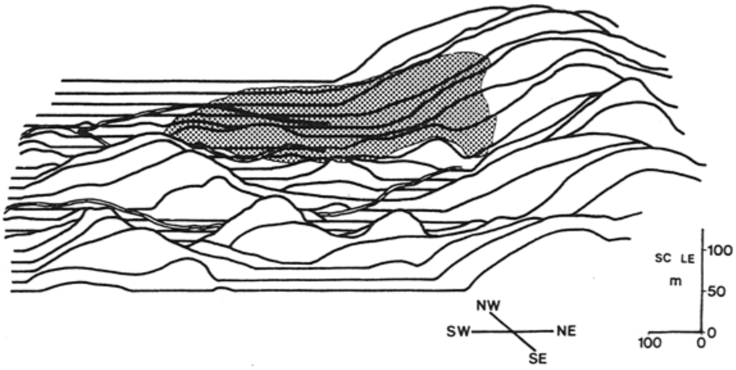

Fig. 9. Diagrammatic cross sections through the study area showing the major rivers and the home range of BG4 (stippled). Distance between sections equivalent to 65 m.

southeast and northwest, where the only barriers to sound are minor ridges. It was possible for him to be heard from the flat areas by virtue of the tall trees he chose for sleeping and the relatively low hills in most of the study area.

The song and display of female Kloss gibbons serve to communicate with neighboring groups. It might be reasonable to suggest, therefore, as Tenaza (1976) has done, that the female song trees are confined to the periphery of the home range, even if they do not delimit it, as he also suggested. To test this, the numbers of trees within two concentric 50-m bands and in the remaining central area were compared with the numbers expected if the distribution were proportional to the area as shown in Fig. 10. No significant difference was found ($\chi^2 = 2.45$, df = 2, $P > 0.05$). Male postdawn song trees were not noticeably peripheral either, although their distribution could not be tested statistically.

The number of female song trees located in each forest type (Whitten, 1982c,d) did not correlate significantly with either the area of or the estimated number of trees in each forest type ($r_s = 0.53$ and 0.60, respectively; $N = 7$, $P > 0.05$, in both cases). The density of female song trees in each forest type did, however, correlate significantly with the density of tall trees and, also, with the median height of tall trees in each forest type ($r_s = 0.75$, $N = 7$, $P < 0.05$, in both cases).

A Kendall partial rank correlation between the density of female song trees and the density of tall trees, with the effects of median height controlled, suggests that the correlation was relatively dependent on the influence of the median height of the tall trees ($r_{\text{fst.tt:mh}} = 0.51$, $r = 0.71$). Conversely, the correlation between the density of female song trees and the median height of tall trees was relatively independent of the influence of tall-tree density ($r_{\text{fst.mh:tt}} = 0.52$, r

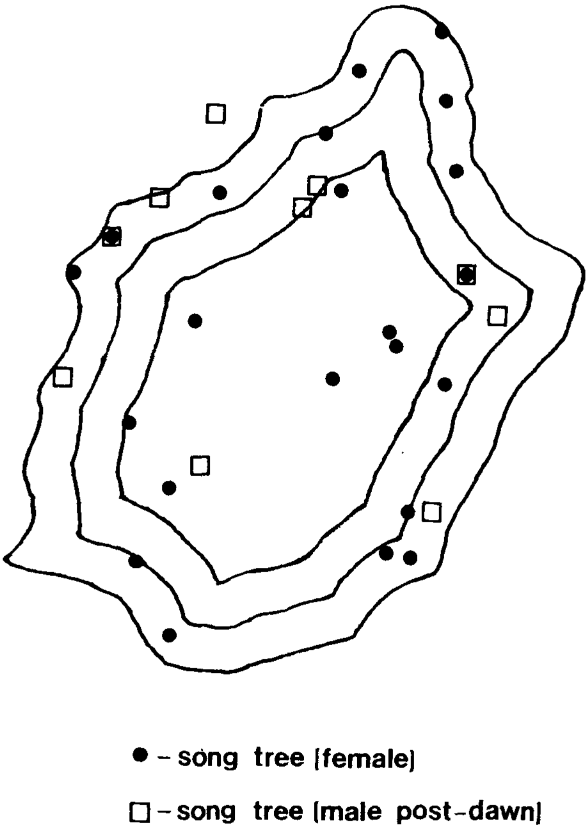

Fig. 10. Position of song trees used after dawn relative to two concentric 50-m-wide bands within the home range. The one male song tree outside the home range was used by the BG10 male on the one occasion he ventured beyond the home range of BG4.

$= 0.62$). These results were somewhat similar to those obtained for night trees (Whitten, 1982c), but there was no significant correlation between the density of night trees and the density of female song trees in the forest types ($r_s = 0.26$, $N = 7, P > 0.05$).

The forest types were related to the height above the surrounding rivers, and the selection of female song trees may have been a function of their elevation. Only 15% of the known female song trees were in the flat, low-lying areas that made up nearly half (46%) of the total home range. There was a significant difference between the numbers of female song trees below and above the break of slope and the numbers expected on the basis of the relative area ($\chi^2 = 9.23$, df $= 1$, $P < 0.01$). It may be concluded, then, that female song trees tended to be in areas above the break of slope and where the trees were tallest.

Singing and Ranging

In general, BG4 traveled twice as far between the first and the last fruit sources on successive days as between fruit sources during the day (Whitten, 1980). The BG4 male sang before dawn every other day on average, but since almost all the days on which he did not sing could be explained in terms of weather conditions, singing would not be expected to be related to any pattern in ranging.

In fact, there appeared to be a direct relationship between singing and the distance traveled to the first fruit source, as shown in Fig. 11. This was confirmed by a Mann–Whitney U test ($U = 118$, $n_1 = 19$, $n_2 = 17$, $P < 0.05$). There was, therefore, a greater likelihood of traveling a long way to the first fruit source on days when he sang before dawn than on days when he did not.

Conversely, there was no significant relationship between singing and the distance traveled from the final, or from the penultimate, fruit source to the night tree when wet nights were excluded from the analyses ($U = 32$, $n_1 = 9$, $n_2 = 9$, and $U = 14$, $n_1 = 5$, $n_2 = 7$, respectively; $P > 0.05$ in both cases).

DISCUSSION

The transmission of sounds through a heterogeneous, complex medium such as tropical rain forest, is quite different from the transmission through homo-

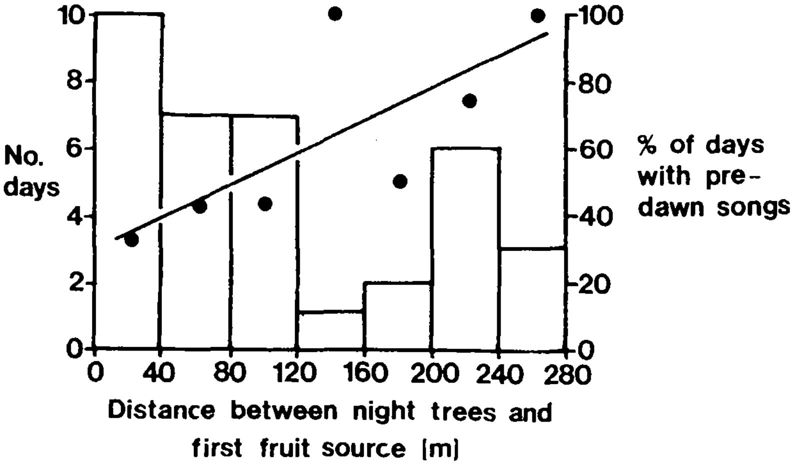

Fig. 11. Distribution of the distance between night trees and the first fruit source (histogram), and the percentage of those days on which predawn songs were given (filled circles and line) ($r = 0.74$, $N = 7$, $P < 0.02$); $N = 36$ days.

geneous nonscattering media (Eyring, 1946; Aylor, 1971). Foliage, air turbulence, temperature gradients, and ground effects can rapidly degrade the structure of a transmitted signal by absorption, reflection, and refraction. This may be particularly severe in tropical rain forest, where all manner of animals from mole crickets to birds, and from monkeys to cicadas, compete for vacant frequencies to communicate with conspecifics.

The general principles concerning the transmission of sounds through tropical rain forest can be summarized as follows:

(1) sounds with wavelengths shorter than objects in the sound path will be reflected, whereas longer wavelengths will not (Stephens and Bate, 1966);

(2) lower-frequency sounds are absorbed less rapidly by humid air than high-frequency sounds (Evans and Bass, 1972; in Waser and Waser, 1977);

(3) vocalizations from sites above the range of ground effects and at times of minimum acoustical interference increase the transmission distance (Waser and Waser, 1977);

(4) complex structural properties of forests produce "sound windows," and at these frequencies sound attenuation is less than at lower or higher frequencies (Morton, 1975); and

(5) temperature gradients, such as those through the forest strata in which temperature increases with height, will refract sound downward, causing it to be trapped and attenuated within the forest (Waser and Waser, 1977).

Sonagrams of tape recordings made of assorted animals at various times during this study revealed the following. The majority of cicadas and orthopterans produced sounds between 3.0 and 5.4 kHz, the only known exception being the loud dawn cicada, which began its call at 2 kHz. The majority of birds with loud songs produced notes between 1.8 and 4.5 kHz. Hill mynahs *Gracula religiosa* L. and Asian fairy bluebirds *Irena puella* (Latham) did start and finish some notes below this, at 0.6 to 0.8 kHz, but generally for less than 0.1 sec. The only bird found to sing at low frequencies was the greater coucal *Centropus sinensis* (Stephens), which repeated single-frequency phrases at 0.3 kHz for about 15 min, generally during the middle of the morning. This call could be heard over several hundred meters. The loud vocalizations of the Siberut monkeys (*Simias concolor* Miller, *Presbytis potenziani,* and *Macaca pagensis* Miller) range between 0.3 and 1.4 kHz (Tilson and Tenaza, 1976; Whitten, 1982f; unpublished data), but few last for more than about 4 sec. The sounds produced by wind and rain have wide frequency distributions (Waser and Waser, 1977), but these elements were relatively rare in the early hours of the morning.

Assuming that the loudness of songs produced by gibbons is limited by their laryngeal morphology, one might expect evolutionary adaptations to reduce attenuation of sounds to ensure maximum transmission distance. That is, a gibbon should ideally produce relatively low-frequency notes in its songs, from sites high above the ground in the few hours before dawn when the temperature gradient between canopy and ground air is least, when few other animals are calling in the same frequency range, and these conditions should be met when the humidity is greatest.

These conditions prevail during the predawn song of male Kloss gibbons. The background noise of other animals is low between 0400 and 0545 hr, after which the dawn chorus of birds builds up. Even so, the 0.4- to 0.9-kHz "channel" remains relatively uncluttered. At dawn, the deafening cicada chorus which drowns most other sounds may be one of the reasons that songs cease during this period, but it is not known how disturbing this chorus actually is to a gibbon in the upper canopy. The loudness of the cicada chorus was not measured, but it is probably comparable to that heard by Waser and Waser (1977) in Uganda, which was also "painfully loud" and was measured at ground level as 70–80 dB.

All the postdawn songs given by BG4 occurred after the first, and often after the second, feeding bout of the day, and the median time of starting was about 0830 hr. By then, of course, ideal conditions have passed, but so too has the fervor of other dawn songs and calls.

When listening to great calls from a distance, it is clear that the trills, which exceed 1 kHz, are more severely attenuated than those notes around 0.8 kHz. It is during the trills, however, that the acrobatic display occurs, and it may be that the female is singing for two audiences, one close with visual and auditory contact and one distant with only auditory contact.

It could be argued convincingly that female songs are not given before dawn because the display is an integral part of the song, and it would be not only dangerous but also pointless to perform such activity in the dark. It is not clear, however, why males should sing after as well as before dawn.

It has been shown that before dawn is an ideal time to call, and it is a matter for debate whether any extra information is given in the postdawn songs that has not been given in predawn songs. Yet, adult males and females appeared to compete for the same broad time slot around 0830 hr in which to sing, as though the male is required to sing at about that time if he is going to sing after dawn at all. This may indeed be the most suitable time after the first feeding bout. Much after this time, the temperature gradient would have increased so that songs would not be transmitted as far, and by the time in the afternoon that the lower canopy temperature has risen to lessen the gradient, the gibbons are starting to enter their night tree.

There appears to be a tendency for a male to sing at least once a day if conditions are suitable. Since postdawn male songs are relatively rare, might they not be interpreted as the result of unsatisfied motivation to sing? The songs would be transmitted further before dawn, but it may be that for a male to sing after dawn is better than not to sing at all. Indeed, male songs were given more frequently after dawn when a song had not been given before dawn than when it had.

The circumstances affecting pre- and postdawn male songs are rather different. The benefits of singing after dawn need to be weighed against the costs of not feeding, discovering new food sources, or patrolling other areas of the home range. During prolonged singing bouts after dawn, the BG4 male was occasionally observed to forage, but never to feed on fruit. Before dawn there is little scope for activities other than sleeping, which anyway forms part of the normal diurnal activity. One might expect, therefore, that predawn songs would last longer than postdawn songs, but it has been shown that there is no significant difference between them in length (Whitten, 1980).

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