



Structure and Use of Distance Calls in Wild Bonobos (*Pan paniscus*)

Gottfried Hohmann¹ and Barbara Fruth²

Received January 15, 1992; accepted January 21, 1993

*We report the physical structure and use of a distance call (high-hoot) by wild bonobos (*Pan paniscus*). Although spectrographic analyses reveal high structural variability, the total sample can be subdivided according to the composition of units—the presence or absence of an initial segment—and the range of the lowest harmonic. Analyses of samples from male–female pairs, vocalizing simultaneously and in close proximity, reveal that both animals utter calls in more or less precise temporal alternation but with different spectral ranges. Whether these differences are gender-specific or related to other factors, such as age or the social relations between particular individuals, is not clear. We suggest that (a) individuals of the same party may coordinate their vocal activity on both the temporal and the spectral level and (b) high hootings stimulate emission of equal vocalizations by members of other parties and may increase cohesion among community members. Comparison of a restricted number of spectrograms from known individuals indicates that bonobos may be able to adjust spectral parameters of one type of distance calls (high-hoot) according to corresponding calls of conspecifics.*

KEY WORDS: *Pan paniscus*; bonobo; vocalization; long-range communications.

INTRODUCTION

Mori (1983) and de Waal (1988) proposed that bonobos (*Pan paniscus*) use various acoustic signals suitable for communication over large

¹Forschungsstelle für Humanethologie in der Max-Planck-Gesellschaft, 82346 Andechs, Germany.

²Zoologisches Institut der Universität München, 80333 München, Germany.

distances including vocal and nonvocal cues. Considering the highly flexible fusion–fission society of bonobos (Kuroda, 1979; Kano, 1992), signals for communication between parties or groups out of visual contact seem to be especially important. However, the physical structure of some of the proposed long-distance calls such as the “high-hoot” (de Waal, 1988) seem to be poorly adapted to long-range transmission. This obvious disparity between physical form and presumed communicative function invites more detailed research on distance communication among bonobos. In contrast to studies of communication among chimpanzees (van Lawick-Goodall, 1968; Marler and Hobbet, 1975; Bauer, 1986; Goodall, 1986), studies of bonobos have been conducted mostly on captive animals (Jordan, 1977; de Waal, 1988; Tröster, 1988; Hopkins and Savage-Rumbaugh, 1991), the advantages of which is that precise knowledge of the subjects’ identities, ages, sexes, and social histories provides an ideal background for assessments of social interactions. Limitations arise however, from the fact that in captivity (a) group composition is artificial, (b) groups are stable and never change in size and composition, and (c) there are spatial restrictions. These limitations may affect severely the use of signals for distance communication. Accordingly, to evaluate the modes and functions of long-distance communication, it is essential to observe subjects living under natural conditions and to collect data when the spatial configuration of the animals involved requires communication over large distances.

Our aim is to provide a clear structural description of different distance calls used by free-ranging bonobos, their utilization in social interactions, and their possible function. We focus on behavioral observations and results of structural analyses of one distance call, previously described by de Waal (1988) as high-hoot. This call is easily distinguished from low-hoots by its tonal quality and is the most common audible vocalization with long-range transmission in the field.

METHODS

Study Site and Subjects

We collected sound recordings and behavioral data between August 1990 and July 1991 in Lomako (Republic of Zaire). The Lomako forest is located in the Upper-Tshuapa district of Equateur, Central Zaire. Details on the location, climate, flora, and fauna of this area have been published by Badrian and Badrian (1984), Malenky and Stiles (1991), and White (1992). Our subjects probably belong to the Eyengo community, which inhabits the eastern part of the Lomako study site (Badrian and Badrian,

1984). During previous research at Lomako, Badrian and Malenky (1984), White (1988, 1992), and Malenky and Stiles (1991) habituated members of the Eyengo community to the presence of human observers. At the beginning of our study, observations were limited to times when the bonobos were engaged in arboreal activities—feeding, foraging, and rest. During the course of the fieldwork, subjects became more tolerant and we could follow parties on the ground for extended periods of time. Until the end of the current field period, we could identify 22 community members (8 males, 14 females) belonging to different age classes via facial features and anatomical peculiarities. We assessed the age of subjects on physical criteria such as body size, development of external genitalia, physiological changes (e.g., cycling), conditions of teeth, mode of locomotion or transport by immature animals, and frequency of participation in specified social interactions. We observed members of the Eyengo community for a total of 239 hr, corrected for simultaneous observations of two observers. Duration of constant observation—visual and acoustic contact with at least one individual—varied between 3 min and 11 hr. Observational distance depended primarily on whether the bonobos were in trees or on the ground and, under the latter condition, varied between 5 and 15 m. While large parties (>10) were easier to detect, the presence or absence of particularly well-habituated individuals had a greater impact on observation time than party size did. Whenever possible, we started observation before the bonobos left the nest site occupied during the previous night. Once we established contact, we continued observations for as long as possible.

Throughout the study period, data collection was opportunistic, involving all possible techniques including *ad libitum* sampling, group scans, and focal-animal sampling. However, we made sound recordings preferably from 11 well-habituated community members—5 males and 6 females—that are a fraction of the entire community. In the absence of precise data on age, we classified them as mature via body size, development and condition of teeth, and size of the testes or genital swelling. During the first months of fieldwork, it was difficult to identify community members. Consequently, we do not address the methodological feasibility and potential significance of physical markers of distance calls.

Our evaluations on the transmission of distance calls are based on simultaneous observations of different parties by two observers. On 33 occasions, as we followed different parties, we noted the approximate location and time of vocalization whenever distance calls could be heard. Later, we assessed the distances between different parties at times of vocalization *vis-à-vis* a map of the study area. In 18 cases, calls from one party were also heard by the observer following the other party, and in these cases, the estimated distances between them ranged from 150 to 500 m. In the re-

maining cases, in which we heard no extra focal group calls, the estimated interparty distances range from 600 to 1800 m.

Technical Equipment

For sound recordings, we used a Sony tape recorder (DAT PCM-2000), Sennheiser directional microphones (ME88, module K3N), and Sony audio tapes (DT-60P). Concurrently with recordings of bonobo vocalizations, we recorded information on the context of interactions and the subjects involved as spoken protocols via a dictaphone. We analyzed the physical structure of the calls by spectrograms produced on a FFT digital real-time analyzer (MEDAV MOSIP 2000/V-2.5) using a Hanning 512 window and a 10-kHz frequency scale. We measured the lowest harmonic on a 5-kHz scale with a Hanning 512 window, providing a sampling rate of 12.8 kHz and a frequency resolution of 25 Hz.

Terminology

For description of the acoustic properties of the calls, we adopted part of the terminology introduced by Struhsaker (1967) and de Waal (1988). Accordingly, *high-hoots* are tonal units consisting of discrete frequency bands (harmonics). Units may be simple (one element) or compound (two sequential elements) and given singly or in phrases. *Phrases* consist of several units with the same structure (uniform) or different structural features (mixed) produced by the same individual. *Choruses* contain a number of phrases from different individuals, uttered more or less simultaneously.

RESULTS

General Description

We tentatively classified tape recordings of high-hoots in the field protocols according to their acoustic impression. We confirmed this classification by inspecting sonagrams and comparing our data with those of de Waal (1988). All samples classified as high-hoots were tonal calls uttered at a comparatively high amplitude by animals of both sexes and all age classes except dependent infants. Although we heard single hoots, they were usually given in phrases containing between 5 and 27 units. Phrases were either uniform, consisting exclusively of high-hoots, or mixed, com-

bining high-hoots with phrases of low-hoots, screams, and sounds produced by drumming against trees.

To get some ideas of the transmission distances of high-hoots, two observers simultaneously listened to different parties. It appeared that the range of transmission of high-hoot choruses at the forest floor never exceeded 500 m.

High-hoots were uttered from all possible body postures, during rest as well as locomotion and from all possible elevations (0–50 m). Occasionally, males accompanied their distance calls with bipedal displays.

Physical Structure

Our data on sound structure are based on analyses of 967 sonagrams of high-hoots. For assessments of the structural features of single units, we measured 13 physical attributes (Table I). Considering the general physical design of units, we distinguish two types of high-hoots. The majority (88.8%) of them is tonal units with a single segment. They started with a low onset frequency that increased rapidly and then descended at or below the onset level (Fig. 1). The remaining samples are compound units where the rising onset was preceded by a tonal initial segment (IS) of lower frequency (Fig. 1). Results of the basic structural features based on standard measurements of 907 single units are given in Table II.

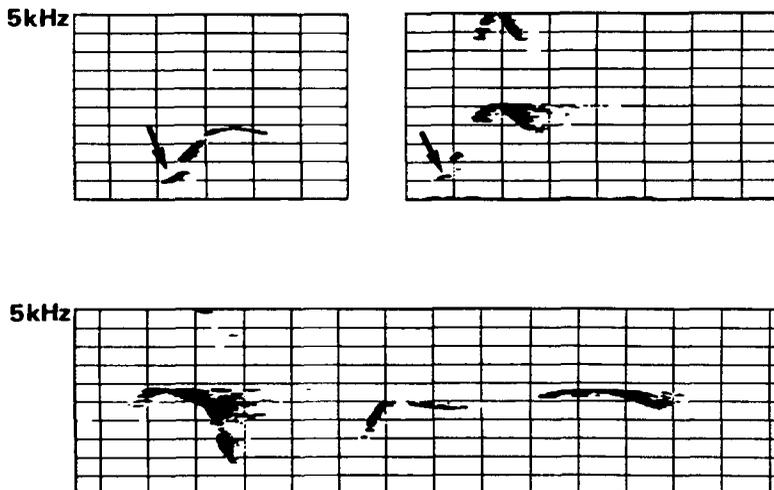


Fig. 1. Five high-hoot units given by adult males. Three units (top left and right) are preceded by an initial segment (arrow), not present in the other unit. Frequency scale, 500 Hz; time scale, 100 msec.

Table I. Description of Attributes used for Analyses of High-Hoots^a

LH minimum	Spectral range of the lowest harmonic (LH) frequency band (mbc)
LH maximum	Spectral range of the lowest harmonic (LH) frequency band (mbc)
LH range	Difference between LH minimum and LH maximum (cal)
LH duration	Time between onset and offset of the lowest harmonic frequency band (mbc)
IS minimum	Lower spectral limit of the low-frequency initial segment (IS) preceding some of the hoot units (mbc)
IS maximum	Upper spectral limit of the low-frequency initial segment (IS) preceding some of the hoot units (mbc)
IS range	Difference between IS minimum and IS maximum (cal)
IS duration	Time between onset and offset of the IS (mbc)
EM minimum	Lower limit of the spectral energy maximum (EM) within the whole unit (mbc)
EM maximum	Upper limit of the spectral energy maximum (EM) within the whole unit (mbc)
PP absolute	Position of the local frequency peak (PP) measured from the onset of the unit (mbc)
PP relative	Position of the local peak (PP) as a percentage in relation to the total duration (100%) of the unit (cal)
IP-interval	Time interval between units within a given phrase emitted by the same individual (mbc)

^ambc, assessment made by measurements with the cursor at the screen of the sonograph; cal, values calculated from the cursor readings.

There is a high variability in both temporal and spectral features of high-hoots (Table II). This is most obvious for the intervals between units produced by the same individual, the duration and spectral range of the lowest harmonic, and the relative position of the local frequency maximum (peak position) of this frequency band. Further analyses indicate a comparatively high correlation between unit duration and peak position (Spearman correlation coefficient 0.7051, $n = 886$) and a moderate correlation between duration of initial segment and peak position (0.5542, $n = 266$).

We heard all acoustic signals with long-range transmission from both males and females. Spectrograms of high-hoots by males and females vocalizing in close proximity reveal that there is a very short delay between the first and the second animal and units are usually emitted in more or less precise alternation (Fig. 2). However, analyses of high-hoots from adult males and females indicate pronounced differences in some physical features (Table II). This is obvious with respect to the position of the lowest harmonic (Table II): In adult female calls ($n = 150$), the mean value of the lowest harmonic is significantly lower than in calls from adult males ($n = 199$) (2299.50 vs 2618.84 Hz; χ^2 , $P = 0.000$). However, separate analyses of male samples reveal that they also produce high-hoots within the range

Table II. Mean Values and Standard Deviations (in Parentheses) of Structural Attributes of High-Hoot Units^a

Attribute	Females (<i>n</i> = 150)	Males (<i>n</i> = 215)	Total (<i>n</i> = 907) ^b
LH minimum (Hz)	996.98 (477.12)	942.88 (423.66)	965.03 (446.47)
LH maximum (Hz)	2299.50 (585.58)	2618.84 (535.99)	2487.60 (577.94)
LH range (Hz)	1300.00 (618.84)	1675.95 (691.82)	1522.06 (687.43)
LH duration (msec)	234.27 (111.77)	249.32 (121.18)	243.14 (117.48)
IS minimum (Hz)	516.11 (201.87)	578.90 (167.00)	571.27 (181.36)
IS maximum (Hz)	812.98 (227.00)	990.54 (271.72)	925.97 (234.42)
IS range (Hz)	318.79 (122.20)	329.54 (149.10)	354.70 (174.32)
IS duration (msec)	72.53 (25.56)	63.32 (20.32)	67.57 (23.23)
EM minimum (Hz)	1600.82 (609.87)	1698.40 (515.12)	1674.80 (579.63)
EM maximum	2019.13 (712.12)	2850.04 (1041.0)	2541.35 (1104.3)
PP absolute (msec)	164.87 (61.19)	105.09 (70.54)	119.48 (77.72)
PP relative (%)	43.19 (13.89)	43.87 (13.12)	43.59 (13.42)
IP interval (msec)	264.21 (155.54)	414.80 (595.78)	356.02 (480.33)

^aFor description of the attributes see Table I.

^bIncludes calls from identified males and females as well as calls from nonidentified individuals.

of females (Figs. 3 and 4). Moreover, our samples (*n* = 38) of male hoots with a low harmonic (≤ 1 kHz) are from individuals calling alone.

Another difference became apparent when analyzing the duration of intervals between units of the same phrase (see values of IP intervals in

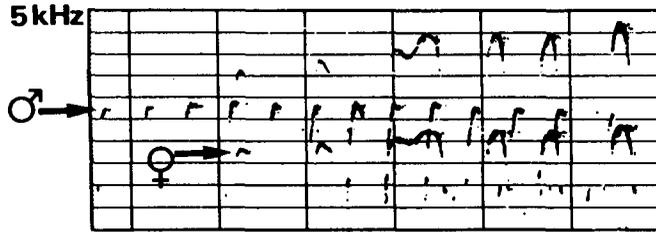


Fig. 2. Sonagram of two high-hoot phrases given by a mature pair vocalizing in unison. The phrase of the male (♂) consists of 13 units, with the lowest harmonic band ranging between 2 and 3 kHz. The phrase of the female (♀) consists of 6 units, with the lowest harmonic ranging between 1.7 and 2.4 kHz. Note the variability of the structure of units and length of intervals in the female phrase. Frequency scale, 500 Hz; time scale, 1.0 sec.

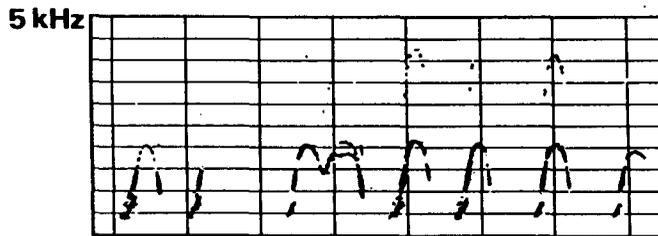


Fig. 3. Sonagram of a solo phrase given by the same male individual as shown in Fig. 2. Note the comparatively low position of the lowest harmonic, which is close to that of the female phrase in Fig. 2, and the structural variation not seen when males vocalize in unison with females. Frequency scale, 500 Hz; time scale, 1.0 sec.

Table II): In phrases of females, intervals were significantly shorter compared with those of males (264.21 vs 414.80 msec; χ^2 , $P = 0.0047$).

Diurnal Distribution and Context of Vocalization

Distance vocalizations of bonobos often coincided with corresponding calls of conspecifics, loud calls of mangabeys (*Cercocebus aterrhymus*) and other less specific noises such as thunder or falling trees (Fig. 5). Field observations made clear that the emission of high-hoots were communal actions, involving most or all members of a group or party. High-hoots could be heard at all times of the day and also at night. However, analyses of the diurnal distribution of high-hoot choruses ($n = 679$) revealed two distinct peaks, one in the morning and another in the afternoon (Fig. 6).

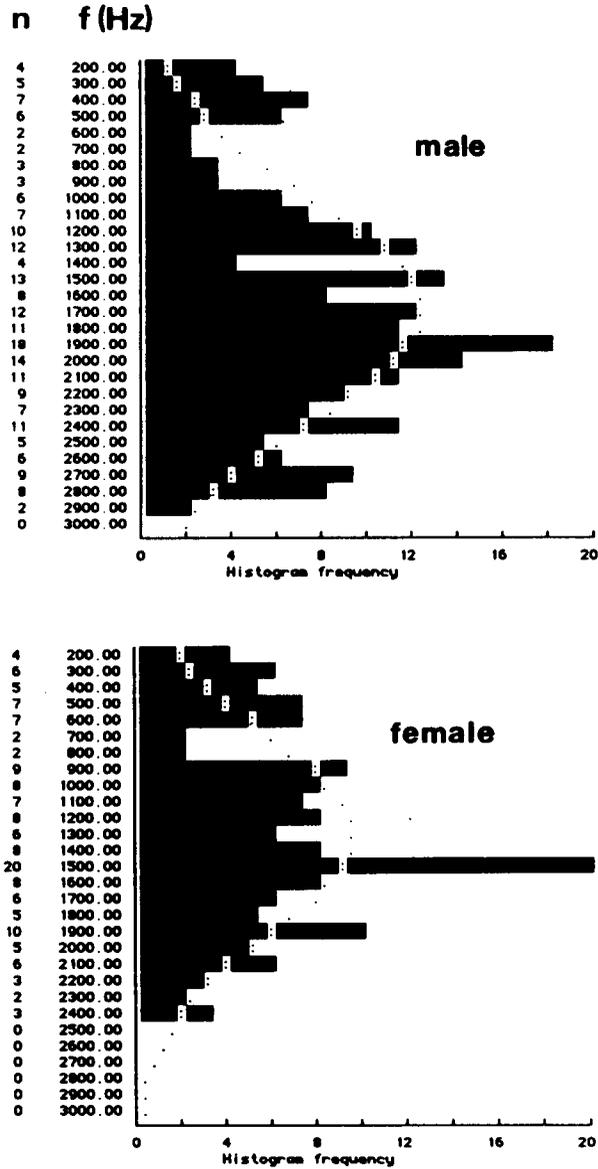


Fig. 4. Distribution and frequency of units according to the position (midpoint) of the lowest harmonic frequency band. The histograms show that, independently of the sex of the vocalizer, samples can be divided into a cluster of units with small ranges (200–600 Hz) and into a cluster of units with medium and large ranges (900–2400 Hz). Only males gave units in which the range of the lowest harmonic exceeded 2400 Hz. n = sample size; f = midpoint position of the lowest harmonic in Hz.

According to field notes on behavioral activities, the first vocal peak coincided roughly with movements between and arrival at different feeding sites (Hohmann and Fruth, unpublished data). However, at that time of the day, vocal activity appeared to be affected by several interrelated factors, like seasonal changes in food availability, party size, party composition, and daily travel distance, and consequently varied considerably. The vocal activity late in the afternoon was more predictable. The afternoon peak closely connected with travel toward and occupation of a prospective nesting site.

Evaluations of the behavioral responses of bonobos to high-hoot choruses of distant conspecifics show that animals gave corresponding calls in >50% of cases (histograms B and C in Fig. 7). Locomotion, with or without vocalization, is the second most frequent response, accounting for approximately 40% of cases. Nevertheless, field observations also demonstrate that in 25% of cases ($n = 38$), parties within earshot did not respond to distant choruses.

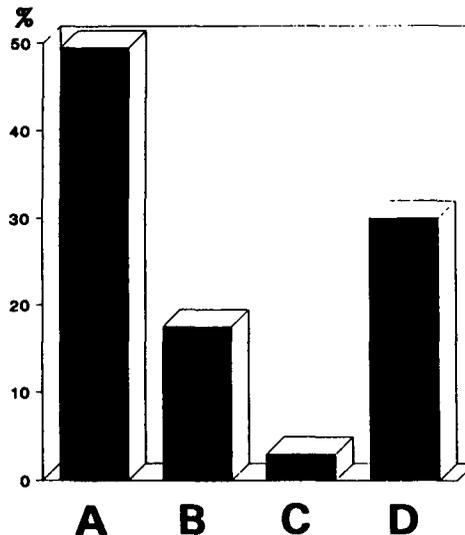


Fig. 5. Assumed releaser for high-hoot phrases or choruses ($n = 621$): (A) corresponding calls (including high-hoot and low-hoot) of conspecifics; (B) loud-calls of mangabeys; (C) other sounds (e.g., thunder, falling trees). In 33% of the cases observed (D) high-hoots were not preceded by other vocalizations and are assumed to have been given spontaneously.

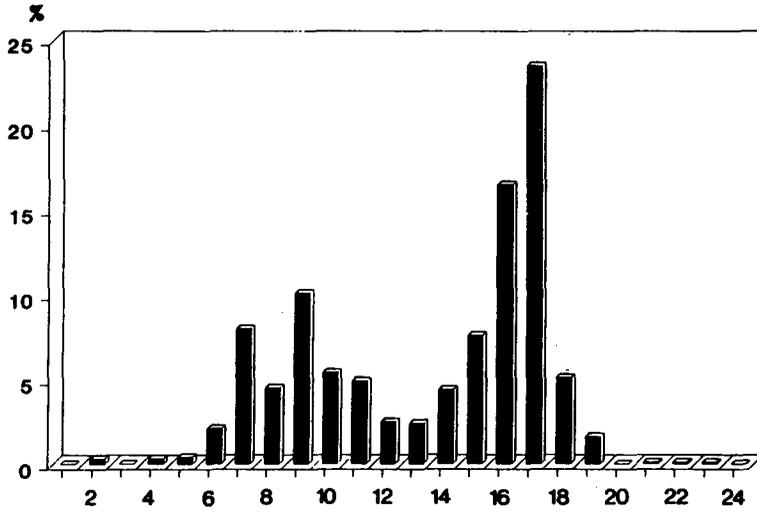


Fig. 6. Diurnal distribution of 679 high-hoot choruses. We heard night choruses only when a party nested close to the camp; they were not recorded systematically.

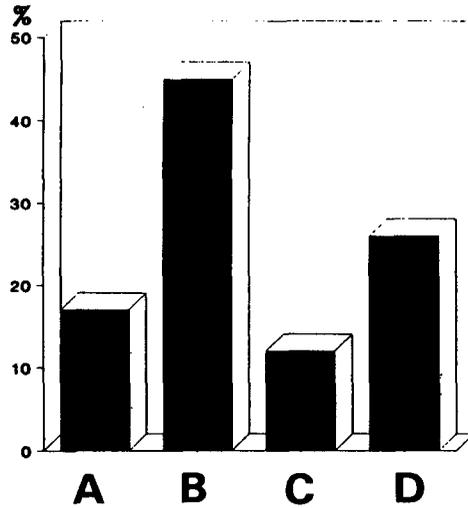


Fig. 7. Response of focal animals/parties to high-hoots from conspecifics out of sight during simultaneous observations ($n = 33$). (A) Silent locomotion; (B) corresponding calls (high-hoot and low-hoot); (C) distance calls and locomotion; (D) no acoustic or motoric response.

DISCUSSION

Studies in the field (Mori, 1983) and captivity (de Waal, 1988), led to the conclusion that high-hoots of bonobos facilitate long-distance communication. By empirical research on vocal communication of rain-forest-dwelling primates, Waser and Brown (1984) documented the existence of "sound windows" and corresponding structural features in vocal signals. Bonobos are able to produce calls of low frequency, e.g., low-hoots. They have large internal air sacs (Rietschel and Kleeschulte, 1989), which probably are used for amplification of vocalizations. However, high-hoots, with their elevated position of dominant frequency (lowest harmonic ranging at approximately 2.5 kHz), seem to be poorly adapted to long-distance communication.

The maximum distance at which we perceived high-hoots of bonobos never exceeded 0.5 km. However, comparison of the time of vocal activity recorded by two observers during simultaneous observations of different parties suggest that bonobos may perceive choruses given at longer distances. Audiograms of chimpanzees show two distinct peaks of high sensitivity (one at 1 kHz, another at 8 kHz) separated by a midfrequency dip ranging between 2 and 4 kHz (Kojima, 1990). From investigations on the radiation of acoustic signals, we know that high-frequency sounds have a higher directionality than low-frequency sounds do (Brown, 1989). Hence, rather than maximizing the distance of signal transmission by matching the lower or upper peak of auditory sensitivity, high-hoots of bonobos may enhance detection of the location of the sender. This does not mean that high-hoots do not serve long-distance communication. Among the seven long-range calls of rain forest monkeys studied by Brown (1989), only three matched the range of the "sound window" that is responsible for superior propagation. Other physical properties may compensate for the loss of transmission caused by the spectral characteristics of high-hoots, and we have to know more about both the spectral characteristics of ambient noise in the Lomako Forest and the perceptual abilities of bonobos.

Some of our results of structural analyses of high-hoots from the bonobos of Lomako are similar to those of studies on captive animals (Tröster, 1988; de Waal, 1988). As in the study by de Waal (1988), Lomako bonobo high-hoots could be separated into two categories or classes, depending on the presence or absence of the initial segment (IS). In contrast to the former study, this trait is not correlated with the attribute peak position in our recordings. Instead, ongoing analyses of calls from Lomako bonobos strongly suggest that the initial segment is a separate element in the vocal repertoire of *Pan paniscus* when uttered both alone and in combination with other calls. Besides the discrepancy in presence and absence

of the IS, the high correlation index between unit duration and peak position accords with de Waal's (1988) description. As shown in Table II and Figs. 2 and 3, within a given phrase, the position of the local frequency peak may change dramatically. In addition to being an attribute suitable for division of the repertoire, peak position also may facilitate identification of the substructure of individual phrases. Such identification of substructures would indeed be comparable to components organizing phrases in human music (Roberts, personal communication).

Differences become apparent when comparing our results with data collected from another study site (Mori, 1983). The first concerns another distance vocalization (low-hoot); the second, the mode of exchange of high-hoots. At Lomako, bonobos give low-hoots consisting of voiced inhalation and exhalation, and at both sites, phrases of low-hoots often precede or accompany phrases of high-hoots. De Waal (1988) reported the latter for bonobos at the San Diego Zoo. In contrast, Mori (1983) stresses that Wamba bonobos do not utter low-hoots. Instead, they "respond to the 'hoot' of other temporary groups with 'wraah'" (Mori, 1983, p. 496). Recall that at Lomako, bonobos responded to high-hoots of conspecifics with corresponding vocalizations in >50% cases. In the absence of any information on the structure of the calls at Wamba, dimensions of site-specific differences still remain speculative.

From analyses of simultaneous high-hootings of mature pairs, it became apparent that calls of both apes were given often in more or less perfect alternation, indicating a remarkable degree of behavioral coordination between them. Jordan (1977) and de Waal (1988) mention a high degree of synchronization between vocalizations of different individuals, and the latter author emphasized the gibbon-like nature of long-distance hooting. It is surprising, however, that the pronounced sexual differences in distance vocalization of wild bonobos have not been mentioned in any of the captive studies. Various explanations are possible, the most simple being that—for whatever reason—samples selected for spectrographic analyses are solos from males and females. Both sexes are able to produce calls in a wider frequency range (Fig. 4) and sex-specific differences of spectral distribution are most obvious in recordings from pairs that vocalize in unison and in close proximity. The reason calls of females are often lower in frequency than the corresponding calls of males is unknown, but this resembles reports from loud calls of Kloss' gibbons (Tenaza, 1976).

The shift of frequency in different phrases of the same individual, which we found in some of the recordings (Figs. 2 and 3), suggests that the utilization of different spectral ranges was intended at least by one individual. This is hypothetical and has to be tested empirically. Recall that the calls that we analyzed were recorded preferably from well-habituated

individuals. Our data on party composition, proximity, and quality and frequency of social contacts collected clearly indicate strong social ties among some of these individuals (Hohmann and Fruth, unpublished data). Hence, it is assumed that the temporal coordination between vocalizations of males and females and the use of different spectral ranges may not express a general gender specificity but, instead, may be related to the specific social relation between particular individuals. If this assumption is correct, high-hooting choruses of these male-female pairs are characterized by parameters that are typical components in the duets of birds, including partner selectivity, precision of timing, and motivational adjustment (Wickler and Seibt, 1982).

In the absence of data on the age of the individuals of the Eyengo community, we cannot deny that some of the structural differences described above are related to age or individuality or both, instead of sex. However, considering the degree of structural variation of units within a sequency of a given individual and the intraindividual variation demonstrated by the samples from one and the same individual (Figs. 2 and 3), it seems unlikely that all the differences in the samples obtained from males and females are related to age or individuality or both, but not to sex.

Although more empirical data on the mechanism and function of distance communication in bonobos are required, our study supports the general assumption that high-hoots are part of a system of signals that facilitate communication between members of different parties. The small number of observations available on locomotion and vocal activity of different parties suggests that the calls affect movements and, thus, may regulate proximity between single individuals, groups, or parties. Analyses of data on party size collected during this study make clear that the number of individuals using the same site for night-nesting was usually higher than that of a party during the daytime (Fruth and Hohmann, in press). The peak of distance calls (Fig. 6) coincides with the gathering of different parties at the same nesting site. Hence, in the absence of evidence for competition between animals or parties for nesting sites, we assume that one function of high-hoots is to assemble of a large number of community members. A supplementary function may be the stimulation of distance vocalization by members of distant parties. Gatherings at the nesting site and daily updates of information concerning the locality of other community members may greatly increase potential opportunities for each individual to join other individuals or parties. Consequently, high-hoots may be the major device to regulate and to maintain the social network of the community.

ACKNOWLEDGMENTS

We thank I. Eibl-Eibesfeldt, G. Neuweiler, and D. Ploog for technical support and advice. Thanks are also due to Lombeya Bosongo Likund'elio and Kambayi Bwatshia (Dept. de l'Enseignement Superieur et Universitaire et de la Recherche Scientifique, Kinshasa) and to Zana Ndontoni and Kande Muamba (Centre de Reserche en Sciences Naturelles, Lwiro), who kindly provided permission to conduct fieldwork. The technical and logistic support provided by the German Embassy at Kinshasa, the Gesellschaft für Technische Zusammenarbeit (Kinshasa office), and the Catholique Missions at Kinshasa, Bamanya, Boende, and Befale is gratefully acknowledged. Special thanks are due to H. Dettmann, E. Ott, C. Kühn, P. Laschan, and B. Unger for their generous help and hospitality and to R. Malenky and N. Thompson-Handler for sharing their ideas and experiences with us. We thank Ch. Roberts for musicological discussions and correction of the English text and P. T. J. Casseday and two anonymous reviewers for their comments on early drafts. For assistance in the field we thank J. P. Bontamba-Lokuli, P. Bozena, F. Christiaans, L. Christiaans, and M. Ikala-Lokuli. Financial support was provided by the Max-Planck-Society, the University of Munich, the German Science Foundation (DFG), and the German Academic Exchange Service (DAAD).

REFERENCES

- Badrian, A., and Badrian, N. (1984). Social organization of *Pan paniscus* in the Lomako forest, Zaire. In Susman, R. (ed.), *The Pygmy Chimpanzee*, Plenum Press, New York and London, pp. 325-346.
- Badrian, N., and Malenky, R. K. (1984). Feeding ecology of *Pan paniscus* in the Lomako forest, Zaire. In Susman, R. L. (ed.), *The Pygmy Chimpanzee*, Plenum Press, New York and London, pp. 275-299.
- Bauer, H. R. (1986). A comparative study of common chimpanzee and human infant sounds. In Taub, D. M., and King, F. A. (eds.), *Current Perspectives in Primate Social Dynamics*, Van Nostrand Reinholds, New York, pp. 327-345.
- Brown, C. H. (1989). The acoustic ecology of East African primates and the perception of vocal signals by grey-cheeked mangabeys and blue monkeys. In Dooling, R. J., and Hulse, S. H. (eds.), *The Comparative Psychology of Audition: Perceiving Complex Sounds*, Lawrence Erlbaum Associates, Hillsdale, NJ, pp. 201-239.
- de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. *Behavior* 106: 183-251.
- Fruth, B., and Hohmann, G. (in press). *Comparative Analysis of Nest Building Behavior in Bonobos (Panpaniscus) and Chimpanzees*. In Wrangham, R. W., McGrew, W. C., De Waal, F. and Helene, P. (eds.), *Chimpanzee Cultures*, Harvard Univ. Press, Cambridge, Massachusetts, pp. 109-128.
- Goodall, J. (1986). *The Chimpanzees of Gombe*, Belknap Press of Harvard University Press, Cambridge and London.

- Hopkins, W. D., and Savage-Rumbaugh, E. S. (1991). Vocal communication as a function of different rearing experiences in *Pan paniscus*: A preliminary report. *Int. J. Primatol.* 12: 559-583.
- Jordan, C. (1977). *Das Verhalten zoolebender Zwergschimpansen*, Unpublished Thesis, Universität Frankfurt a.M., Frankfurt a.M.
- Kano, T. (1992). *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*, Stanford University Press, Stanford, CA.
- Kojima, S. (1990). Comparison of auditory functions in the chimpanzee and human. *Folia Primatol.* 55: 62-72.
- Kuroda, S. (1979). The social group of the pygmy chimpanzee. *Primates* 20: 161-183.
- Malenky, R. K., and Stiles, E. W. (1991). Distribution of terrestrial herbaceous vegetation and its consumption by *Pan paniscus* in the Lomako forest, Zaire. *Am. J. Primatol.* 23: 153-169.
- Marler, P., and Hobbet, L. (1975). Individuality in a long-range vocalization of wild chimpanzees. *Z. Tierpsychol.* 38: 97-109.
- Mori, A. (1983). Comparison of the communicative vocalizations and behaviors of group ranging in Eastern gorillas, chimpanzees and pygmy chimpanzees. *Primates* 24: 486-500.
- Rietschel, W., and Kleeschulte, E. (1989). Beitrag zur Erkrankung der Kehlsäcke (*Sacci laryngis*) beim Bonobo (*Pan paniscus*). *Tierärztl. Prax.* 17: 323-326.
- Struhsaker, T. T. (1967). Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In Altman, S. T. (ed.), *Social Communication Among Primates*, University of Chicago Press, Chicago, pp. 281-324.
- Tenaza, R. (1976). Songs, choruses and countersinging of Kloss' gibbons (*Hylobates klossi*) in Siberut Island, Indonesia. *Z. Tierpsychol.* 40: 37-52.
- Tröster, P. (1988). *Kommunikationsverhalten beim Bonobo (Pan paniscus, Schwarz 1929) unter besonderer Berücksichtigung des akustischen Bereichs*, Unpublished thesis, Universität Heidelberg, Heidelberg.
- van Lawick-Goodall, J. (1968). A preliminary report on expressive movements and communications in the Gombe stream chimpanzees. In Jay, P. C. (ed.), *Primates: Studies in Adaptation and Variability*, Holt, Rinehart and Winston, New York, pp. 313-374.
- Waser, P. A., and Brown, C.h. (1984). Is there a "sound window" for primate communication? *Behav. Ecol. Sociobiol.* 15: 73-76.
- White, F. J. (1988). Party composition and dynamics in *Pan paniscus*. *Int. J. Primatol.* 9: 179-193.
- White, F. J. (1992). Activity budgets, feeding behavior and habitat use of pygmy chimpanzees at Lomako, Zaire. *Am. J. Primatol.* 26: 203-214.
- Wickler, W., and Seibt, U. (1982). Song splitting in the evolution of dueting. *Z. Tierpsychol.* 59: 127-140.