

LOUD CALLS IN GREAT APES: SEX DIFFERENCES AND SOCIAL CORRELATES

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INTRODUCTION

If one were to scan the literature on primate behavior accumulated during the last two decades, one single taxon, the great apes, would likely dominate. Switching the key word to "communication" would already decrease the bias drastically, and when selecting for "vocal communication", the taxon would produce a rather marginal file (Marler, 1976; Marler and Tenaza, 1977). Behaving "almost human" in some aspects, there is no evidence that vocal communication by the great apes exceeds that of other non-human primates. This view is certainly biased. Until recently, we knew little about the structure and function of their natural vocal repertoires. Instead, researchers taught chimpanzees sign language and other artificial communication systems (for reviews see Sebeok and Umiker-Sebeok, 1980; Wallman, 1992). These studies may have quantified the cognitive abilities of the subjects but little was learned about the mode of natural communication among conspecifics. The picture is slowly changing. Long term field studies on all four species permit systematic research of vocal communication of focal individuals. Studies of animals in captivity use the advantages of more controlled conditions to evaluate the functional significance of particular calls. In the field, attention focused on elements of the vocal repertoire which are likely to facilitate distance communication. For several reasons this bias is not surprising. First, these *loud calls* are easy to detect by human researchers even against high levels of background noise. Second, because of their high amplitude and other physical adaptations for long-range transmission, loud calls are easy to record. Third, loud calls are of special interest because they are thought to encode and transmit information exclusively in an acoustic manner. Finally, field observations on various primate species have demonstrated that conspecifics' responses to loud calls are both detectable and predictable. This is in contrast to most of the other elements which either elicit no obvious behavioral response or a variety of different responses.

Loud calls are used by many primate species and have been the subject of detailed studies (e.g., Gautier and Gautier, 1977; Zimmermann, this volume). Analyses of primate calls that may facilitate long distance communication have revealed that superior propagation depends on both the energy distribution in the spectrum of ambient noise ("sound windows") and the spectral features of the signals (Brown, 1989; Waser and Brown, 1984). Comparative data from two species (blue monkeys and mangabeys) have also demonstrated a positive correlation between the range of transmission of long distance calls and home range size (Brown, 1989). However, species-specific differences in signal structure have been attributed to differences in competition between males rather than to differences in the acoustic environment (Waser, 1982). The classification of a vocal signal as a "loud call" is normally based on several criteria including intensity (sound pressure level), structural originality and low variability in structural features (Gautier and Gautier, 1977). There are only few studies in which the sound pressure level of primate loud calls was measured (e.g., Brown, 1989; Whitehead, 1987) and in most species (including all the great apes) evaluations of the intensity were based on subjective judgements of a human listener. Evaluation of the extent of structural variability of a particular call requires samples from a large number of different subjects, and samples of the same individual collected during a longer period of time. For some species, these data are available (e.g., Gautier and Gautier, 1977, for forest guenons and Deputte, 1982, for gibbons). However, they are not available for the four species of great apes.

In spite of their high intensity, loud calls may not always facilitate long distance communication but have a relatively short audible range (Brown, 1989). The calls selected for this comparison are among the loudest produced by the given species and can be heard by observers on the ground several hundred meters away from the source. Nevertheless, it is important to emphasize that other calls produced by each species may carry further, and experience less degradation and less attenuation than the samples selected here. Comparing the audible range of vocal signals with home range size of mangabeys and forest guenons, Brown (1989) was able to distinguish "public calls" from "private calls". One could probably do the same with gorillas who live in coherent harem groups. Considering the fission-fusion society of chimpanzees and bonobos the distinction between the two categories would be more difficult. In orangutans, all vocalizations (except for calls used for communication between mother and dependent offspring) would be scored as "public" signals. In the absence of empirical data on both, the vocal signals and the acoustic environment we will use the terms "loud call" and "distance communication" in a conventional way.

The following paper reviews results of current studies on loud calls in the four great ape species. In addition to reviewing written work, we present the first data from bonobos collected by the authors during an ongoing field study at Lomako (Zaire). Special attention will be given to the various hypotheses concerning the potential function of these calls in the different species. We also examine sex differences in the use of loud calls, focusing on the question of why females of some species refrain from loud calling while females of other species participate in this activity. To complement the great ape data, we also address this question using data from simian primates. The hypothesis we propose can be tested more systematically in future projects. Provided this happens, we will have achieved the major goal of this paper, that is, to stimulate greater interest in a previously neglected subject, the significance of female loud calls.

For description of the acoustic properties of the calls, we adopted part of the terminology introduced by Struhsaker (1967) which contains the following elements: unit (tonal, non-tonal), phrase and bout. Tonal units consist of discrete frequency bands, while non-tonal units are characterised by their diffuse spectral distribution. Units may be simple (one element) or compound (two elements follow one another). Phrases consist of several

units with the same structure (uniform) or different structural features (mixed) produced by the same individual. Bouts are clusters of phrases given by one and the same individual. In contrast, choruses consist of a number of phrases from different individuals uttered more or less simultaneously.

LOUD CALLS OF GREAT APES

Orangutan

There is little information on vocal communication in orangutans and the only vocalization which has been subject to more detailed studies is the *long call* (Galdikas, 1983; Galdikas and Insley, 1988; MacKinnon, 1974; Mitani, 1985).

Structure (Table 1): The term *long call* refers to phrases of units with different physical features. It starts with pulsed grumbles, continues with bellows, and trails off with grumbles and sighs (Galdikas and Insley, 1988; MacKinnon, 1974). There might be individual markers because human observers, familiar with the subjects, were able to identify the different males by their long calls (Galdikas, 1983; Mitani, 1985). Galdikas and Insley (1988) distinguish a second type of distance call, the *fast call*. Compared with long calls, fast calls were uttered less frequently (1.7% of all long calls), structural variation within fast calls seemed to be less pronounced, phrases were of longer duration and units were emitted at a higher rate.

Site Specificity: As a prelude to their long calls, males from Tanjung Puting (Central Kalimantan) push over large branchless trees (Galdikas, 1983). Originally, it was proposed that this peculiarity is unique to this site. However, in Kutai Game Reserve (East Kalimantan) the noise of falling branches was always followed by long calls (Mitani, 1985), indicating that at least the connection between this external stimulus and long calls is not restricted to the population of Tanjung Puting.

Context: Empirical data on the context of long calling are available from studies at Tanjung Puting (Galdikas, 1983; Galdikas and Insley, 1988) and from Kutai (Mitani, 1985). At both sites the vast majority of samples (93% at Tanjung Puting and 82% at Kutai) were given spontaneously. Loud noises caused by falling trees or long calls of conspecifics evoked corresponding calls, too. Encounters between adult males were the most reliable releaser for long calls. With one exception, all encounters were characterized by aggressive interactions, and it was the dominant individual who gave long calls. Males not visible but calling in close proximity also increased the rate of vocalization by the dominant male. Mating seems to be another context for long calling. Most copulations observed (87% at Tanjung Puting, 67% at Kutai) were preceded or accompanied by long calls. Galdikas (1983) observed that long calls by adult males often (43%) evoked proceptive behavior in adolescent females and that receptive adolescent females were locating (and approaching) adult males by their long calls. She suggested that initiation of contact with other individuals was the major stimulus for long call vocalization. Conversely, Mitani (1985) found that males called most frequently following associations between males and females. Since the fast calls given by male orangutans at Tanjung Puting have been characterized as a "post-conflict" vocalization (Galdikas and Insley, 1988), this disparity could be a matter of definition rather than a site-specific pattern. Both studies have demonstrated that the response to long calls varies with the distance between sender and receiver. In Tanjung Puting, focal animals showed visible responses most often when the distance of the

vocalizer was below 400 m. In Kutai females associated with adult or subadult males moved away from the loudspeaker even at distances above 400 m. Observations from both sites suggest that the response of males does not depend solely on the distance between sender and receiver but is also an expression of the dominance relationship between the two individuals. The motoric response (approach-avoidance) of three adult males from Tanjung Puting towards long calls given within the spatial limits of 400 m indicated a linear hierarchy.

Function: It has been hypothesized that male long calls have two different functions: spacing among males and mate attraction. Both functions are not mutually exclusive but may in fact complement each other. To test both hypotheses, Mitani (1985) conducted a series of playback experiments. Tests of the male-spacing hypothesis included the following: (a) playback of a long call from the dominant (resident) male to 4 subordinate (non-resident) adults and 4 subadults, and (b) playback of a long call given by a subordinate (non-resident) adult to the dominant male. In response to playbacks of the long call from a subordinate adult, the counter-calling dominant male approached the playback site. Hearing the long call of the dominant male, subordinate adults and subadults silently moved away from the location of playback and moved with a faster speed than before the experiment. To test the mate-attraction hypothesis, a long call of the dominant male was presented to (a) 3 adult females with infants and (b) 2 adult females without infants but accompanied by subadult males. Following the playback, females remained stationary or avoided the adult male. These data do not support the mate-attraction hypothesis but are not sufficient to reject it completely (Mitani, 1985).

Gorilla

Recent studies on vocal communication of gorillas have focused on calls used for communication over short distances (Harcourt et al., 1986, 1993). Information on distance communication has come from studies on mountain gorillas by Schaller (1963) and Fossey (1972). Out of 22 different vocal patterns distinguished by Schaller (1963), four may serve communication over large distances. Fossey (1972) described 16 types of vocalization including the *roar*, *wraagh* and *hoot series*. Both studies agree that roars and hoot series are given almost exclusively by silverback males and are usually followed by aggressive displays. Wraaghs in contrast are given by members of all age/sex classes (except infants) and are not accompanied by aggressive displays. Hoot series are that gorilla loud call with the highest similarity to loud calls of the other great apes.

Structure (Table 1): Hoots are tonal or mixed units usually given in phrases (hoot series) consisting of up to 20 units. Considering differences in duration of units and intervals, Schaller (1963) distinguished two different sections (hooting and growling) within a phrase. Hoot series are frequently terminated by other acoustic cues like chest beating, ground thumps and branch braking.

Context: Hoots were given exclusively during encounters with other groups or lone males (Fossey, 1972; Elliot, 1976). During close encounters (600 m or less) hoot series were more likely to be terminated by displays (chest beat, parallel run). The most common releaser for hoot series were corresponding vocalizations from other males. Group members responded to hoots with dispersion.

Table 1. Some structural features of loud calls of great apes (references are given in the text).

Species	Type/ section	Fundam. frequency (Hz)	Duration of unit (sec)	Units per phrase	Phrase duration (sec)	Transmiss. range (km)
<i>Pongo pygmaeus</i>	long call			18	14.1	0.8
	- grumbles	100-500	0.01-0.05			
	- bellows	100-1200	0.13-1.63			
	- sighs	100-600	0.13-1.30			
	fast call	?	?	34	54.7	?
<i>Gorilla gorilla</i>	hoot series	100-700 1400-1800	0.03-0.20	>20	6.8	?
<i>Pan troglodytes</i>	pant hoot			23	2.0	0.6
	- introduction		?			
	- build up	250-350	0.15-0.25			
	- climax	600-1400	0.40-1.00			
	- led down					
<i>Pan paniscus</i>	low hoot	500	0.10-0.27	5-17	1.2-4.5	0.3
	high hoot	2300	0.15-0.70	4-41	1.5-5.8	0.5

Function: Observations on the context of emission of hoot series have indicated their significance for intergroup communication. Field observations gave the impression that the members of a given group responded differently (retreat or approach) to hoot series from different silverbacks (Akles, cited in Fossey, 1972) suggesting that conspecifics may be able to recognize the identity of the vocalizer by voice. Changes in spacing might be the most important consequence of hoot series, but the data available are not sufficient to determine if the function is primarily distance-increasing, distance-maintaining, or both.

Chimpanzee

The vocal repertoire of chimpanzees includes a number of calls for long range communication (Goodall, 1968, 1986). Among those, *pant hoots* are one of the most frequently uttered calls of adult chimpanzees. They are given by males and females of all age classes and can be heard during all hours of the day and from nesting sites at night (Goodall, 1986).

Structure (Table 1): Single units consist of a voiced inhalation and exhalation phase and are given in phrases. Within a phrase, different sections can be distinguished (Marler and Hobbet, 1975): (1) the *introduction* with relatively long, unmodulated units, (2) the *build-up* characterised by an increase in both amplitude and range of frequency modulation,

(3) the *climax* consisting of comparatively long units with extensive modulation, and (4) the *let-down* which mirrors the build-up. Phrases can incorporate units of other vocal and non-vocal cues (e.g., shrieks and drumming) and may vary within a wide range according to the identity, age and sex of the vocalizer, and perhaps also with the context of emittance.

Individuality and Rank: Most field-workers agree that pant hoots of different individuals can be distinguished by humans even at large distances. Marler and Hobbet (1975) provided the first detailed description of structural differences suggesting various dimensions for individual specificity. However, recent studies suggest that at least some of the individual-specific features are surprisingly flexible. Disappearance of four males from a habituated community observed by Boesch (1991) caused major structural changes in the pant hoots of three other males. One male adopted the style of pant hooting formerly used by one of the missing males. At the same time the alpha male (Brutus) had modified his pant hoots and another male (Falstaff) "...started to produce exactly the long series of rapid hoots that Brutus had used previously" (Boesch, 1991, p. 83). This suggests that certain features of pant hoots could be related to social rank and/or dominance status. More evidence for rank-related differences comes from a study conducted by Mitani and Nishida (1993) at Mahale. In this study, seven adult focal males were ranked according to the outcome of agonistic interactions and the direction of pant grunts. High ranking males gave more pant hoots than low ranking males. While the calls given by the alpha male received the highest rate of vocal responses from other males, the alpha male responded least to the calls of others. However, none of the other six focal males showed the same pattern of vocal activity.

Age and Sex: Individually known chimpanzees of habituated communities have been studied for more than three decades. However, information about the ontogeny of vocal communication is virtually non-existent. Pusey (1990) reported that the rate of pant hooting increases with age and that in the case of females this development seems to be connected to the first estrous. Recordings from Gombe suggest that phrases of older males were shorter compared to phrases given by younger males (Marler and Hobbet, 1975). However, older males were also higher in rank and the structural variation could therefore equally express rank differences.

It is unfortunate that even in the more detailed studies, the pant hoots given by females were - for whatever reason - excluded from analyses (e.g., Mitani and Nishida, 1993; Mitani et al., 1992) or pooled with male calls (Clark, 1991). Hence, the existence of sex differences remains to be demonstrated. One difference between males and females might be the rate of pant hooting. Juvenile females produced pant hoots less frequently and joined choruses less often than male peers (Pusey, 1990). Figures on vocal rates from several other studies indicate a similar tendency (e.g., Clark, 1991; Marler, 1976; Mitani and Nishida, 1993). However, because of the consistent rank differences between the sexes (males are always dominant over females), it is not yet possible to distinguish precisely between the effects of rank and sex.

Site Specificity: Samples of male pant hoots recorded at Gombe and Mahale, respectively, have revealed differences in temporal and spectral features (Mitani et al., 1992). Individuals from Mahale, emitted the second section (build-up) of their pant hoots at a faster rate and the climax with a higher pitch than chimpanzees at Gombe. However, any interpretation of these site-specific differences is difficult because the two data sets are not really compatible. In Gombe, recordings were made during a short period of time and only from animals visiting the artificial feeding site. In Mahale, the period of sampling spans 6 years and recordings were collected under natural conditions (Mitani et al., 1992). Both

sites are isolated and genetic differences between the two populations cannot be excluded. Genetic variation could have an impact on anatomical and/or morphological traits which in turn could cause differences in sound production. Alternatively, chimpanzees could acquire their vocal performance through learning and develop site-specific dialects. However, until compatible data sets are available the problem of site specificity remains an open question.

Context: Pant hoots are given in a wide range of diverse and partly disparate contexts (Goodall, 1965, 1986): arrival at a rich feeding site, capture of animal prey, joining of other community members, response to voices of strange conspecifics, and during agonistic displays. However, until recently evidence for context-related structural variation was lacking. According to Wrangham (1977) pant hoots given on arrival at large feeding sites sounded different from pant hoots given in other contexts. The structural attribute that appeared to be related to this specific context is the presence/absence of the last section (let-down) of a phrase. In a study at Kibale Forest (Uganda), Clark (1991) and Clark and Wrangham (1993) analysed recordings from adult males and females visiting fruit-bearing fig trees. They found that a high proportion (43%) of the pant hoots given within 5 minutes after arrival included the let-down section. In samples given more than five minutes after arrival, the proportion of pant hoots with let-downs was much lower (11%) but still higher than in any other context category. Recordings from Mahale did not confirm the findings of Kibale, and it was concluded that the results did not "support the claim that chimpanzees have a distinct vocalization that they give uniquely upon arrival at food trees" (Clark, 1991, p. 91). Nevertheless, the study has demonstrated that the utterance of pant hoots with a let-down section is at least closely connected to the feeding context.

Function: Field observations on the context of pant hooting have raised various propositions about its possible function including (1) intergroup spacing, (2) establishment and maintenance of social parties, (3) attraction of allies, (4) attraction of mates, and (5) food availability (Goodall, 1986; Wrangham, 1977; Wrangham and Smuts, 1980). All of them involve spatial regulation and each single hypothesis is compatible with one or several others. Are there empirical data supporting or rejecting one or the other hypothesis?

(1) Goodall (1986) reported that upon hearing choruses of distant individuals from another community, chimpanzees move either away from the source of sound or engage in vigorous displays. Apparently, assessments of the number of males present in distant parties were based on pant hoots and drumming. Although the effect of pant hoots for inter-community spacing should be tested more rigorously (e.g., with playback experiments), there is at least some indirect evidence in support of the first hypothesis.

(2) Evidence for the proposed function of coordination between parties of the same community comes from the Tai forest where Boesch (1991) collected data on distance communication from the alpha male of a habituated community. The study focused on sequences of pant hoots, drumming and climax screams. The observations suggested that the response of other community members depended on the repetition of sequences within 2 minutes or less, and the location of repeated sequences. Depending on the spatio-temporal design of the performance, the behavior of the alpha male following his own performance, and the behavioral response of other members, human observers distinguished three different types of messages: (a) change of travel direction, (b) announcement of a resting period, (c) a combination of both. Boesch (1991) concluded that some of the pant-hoot-drumming sequences of Tai chimpanzees transmitted precise information to other community members and that this communication system can partly function in a symbolic way. These data provide support for the second hypothesis.

(3 and 4) Recently, Mitani and Nishida (1993) have investigated the influence of several social factors on the production of pant hoots by adult males. In this study, two

aspects were considered: the size of the party to which the focal males belonged, and the proximity of focal males and particular social partners (*allies*, *associates* and *estrous females*). Vocal activity of the different males was measured for three different conditions (*within*, *nearby* or *far away* from the focal male). The results suggested the following: First, there was no correlation between party size and vocal activity of the focal males. Second, focal subjects called more often when allies and association partners were nearby than when these individuals were absent. Third, the two highest ranking males and one middle ranking male called more frequently when estrous females were nearby than when absent. Finally, the three low ranking males called less often when estrous females were nearby.

These findings support the third hypothesis, indicating that pant hoots of adult males may facilitate communication with allies and associates in order to maintain contact and/or recruit aid. However, the mate attraction hypothesis remains to be tested again (Mitani and Nishida, 1993); the authors considered the possibility that the conflicting results "...may reflect the different mating tactics employed by males of varying ranks" (p. 744).

(5) Food experiments conducted in a group of captive chimpanzees have revealed that with one exception, pant hoots were always given by adult males and primarily by subjects who discovered large amounts of food (Hauser et al., 1993). If the aim of food calling is to attract other individuals to a food source, one would expect that animals who vocalize are joined by a larger number of individuals than animals who keep quiet. Studies by Wrangham (1977) in Gombe and Ghiglieri (1984) at Kibale (Ngogo community) revealed that individuals giving food calls were joined more often (33% and 59%, respectively) than individuals not vocalizing (6% and 34%, respectively). Another study in the Kibale forest (Kanyawara community) failed to reproduce these results (Clark, 1991). Hence, the fifth hypothesis (food attraction) can be neither accepted nor rejected.

Bonobo

Until recently, information about communication among bonobos was restricted to brief descriptions of some frequent vocalizations (e.g., Jordan, 1977; Kuroda, 1979; Savage-Rumbaugh and Wilkerson, 1978). Recent studies on captive colonies in San Diego (de Waal, 1988) and Frankfurt (Tröster, 1988) revealed two groups of long distance calls: *low hooting* and *high hooting*. Distance communication among wild bonobos has been described to some extent by Mori (1983) and is now one of the major topics of an ongoing field project at Lomako (Hohmann and Fruth, in press).

Structure (Table 1): Low hoots consist of two phases (inhalation and exhalation) and are always given in phrases (de Waal, 1988). According to spectrographic analyses of high hoots from Lomako (Hohmann and Fruth, in press) and San Diego (de Waal, 1988) several types of high hoots can be distinguished. However, the current classification is still tentative and more data are needed for a useful subdivision of this category.

Sex: Analyses of high hoots from adult males and females collected at Lomako indicated sex differences in some physical features. First, in calls of adult females the average fundamental frequency was significantly lower than in calls from adult males. However, when analysing the samples of males separately, it became apparent that they also produced high hoots within the range of females and that the samples of male hoots with a low fundamental were recorded from lone individuals. In addition, the intervals in phrases of females were significantly shorter than in males (Hohmann and Fruth, in press).

Context: In captivity low hoots were not directed at a particular individual but given in response to environmental changes and disturbances (de Waal, 1988). In Lomako, low

hoots were either directed towards the human observer or elicited by vocalizations of distant community members and were often accompanied by agonistic displays (e.g., stamping on the ground or tree drumming). In Lomako emission of high hoots coincided with corresponding calls of conspecifics (48%), loud calls of mangabeys (16%) and other less specific noises (3%). In the remaining cases, high hoots were given spontaneously (Hohmann and Fruth, in press). In captivity, increased rates of high hooting coincided with the regular feeding times, suggesting that expectation or discovery of food stimulates vocalization. However, measurements of the vocal activity during food experiments suggest that the quantity of food presented to the subjects does not affect the number of high hoots (van Krunkelsven, 1993). In Lomako, high rates of hooting marked the capture of prey, the beginning of food-sharing episodes or invasion of feeding trees. The highest rates of high hooting were scored when different parties gathered at nesting sites.

Function: Although more empirical data on the function of distance communication in bonobos is required, observations from Lomako confirm previous proposals that high hoots are part of a system of signals facilitating communication between members of different parties. The most common response to choruses of distant conspecifics was high hooting (more than 50%) or locomotion (40%). Together with simultaneous observations on locomotion and vocal activity of different parties, this suggests that the basic function of high hoots is the maintenance and/or reduction of distance between different parties. Moreover, data from Lomako revealed that the number of individuals gathering at the same nesting site for the night was consistently higher than in day parties (Fruth and Hohmann, in press). In the absence of any evidence for competition between individuals or parties for nesting sites, it is assumed that one specific function of high hoots is the assemblage of a large number of community members at nesting sites.

DISCUSSION

Reviewing loud calls of the great apes reveals correspondence in a number of patterns. Loud calls always occur in phrases consisting of more or less distinct sections, and the vocalizations were often combined with acoustical cues. In all species, the calls were given by adult males and in those species where relevant data are available, dominant individuals vocalized more often than subdominants. The majority of loud calls were uttered spontaneously or during encounters with conspecifics.

However, comparisons between some of the species revealed great differences. In orangutans and gorillas, loud calls were given exclusively by adult, dominant males and showed a rather stereotype structure (Fossey, 1972; Galdikas, 1983; Mitani, 1985). Behavioral observations and field experiments suggest that in both species spacing among single males or members of different groups is the major function of loud calls.

In chimpanzees and bonobos, mature and immature individuals of both sexes gave loud calls in a variety of contexts, ranging from agonistic to affiliative (Marler, 1976; de Waal, 1988). The bulk of the data consisted of calls used for communication between members of the same community. Spectrographic analyses have demonstrated a high degree of variation in structural features. Some of these features appear to be related to the rank of the vocalizer, whereas others appear to encode specific messages. The sudden structural changes of the pant hoots of three adult males from Tai forest invite speculations about the possibility of imitation of individual-specific and perhaps rank-related features. Studies on bonobos also indicate covariation of certain structural features of high hoots and context of emission. Analyses of sound recordings further suggest that bonobos may be able to adjust

spectral parameters of high hoots according to corresponding calls of conspecifics (for similar observations see Sugiura and Masataka, this volume).

Interspecific differences in vocal behavior may reflect differences in the complexity of social organization or be related to a shift from inter-group communication to intra-group communication. This is precisely the concept adopted by Marler (1976) when comparing the vocal repertoire and vocal behavior of chimpanzees and gorillas, respectively. While comparison of structural features indicated a high degree of correspondence between the two species, striking disparities became apparent when the use of equivalent calls by males and females was considered. Although chimpanzees of different age and sex contributed to the overall production of a given call with different rates, all vocalizations were given by males and females. In contrast, three calls of the gorilla repertoire were heard only from adult males and a number of other calls were also produced more frequently by males than by females. Marler (1976) proposed a correlation between the contrasting patterns of social organization and the related differences in spatial distribution on one hand, and the differences in vocal behavior on the other. Accordingly, the low degree of age and sex differences in vocal behavior in chimpanzees was in line with both the spatial dispersion of community members and the relatively balanced participation of all age and sex classes in social affairs. In gorillas, superiority of vocal behavior by one age and sex class (adult silverback males) corresponded well with the strong cohesion between group members and the social dominance of adult silverbacks. Though the differences in vocal behavior between the two African apes may indeed be related to certain facets of their social organization, the influence of other factors should be considered as well. First, in contrast to the conditions with the chimpanzees at Gombe, the data from gorillas have been collected at the beginning of a long term study when subjects were poorly habituated, and it is possible that the true capacity of distance communication among gorillas has been heavily underestimated. Second, there is good evidence that the patterns of social organization may be flexible within and between populations of the same species (see Byrne et al., 1990, for baboons; Milton, 1984, and Strier et al., 1993, for woolly spider monkeys; Watanabe, 1981, for pigtailed langurs) but corresponding modifications of vocal communication have yet to be demonstrated. Third, chimpanzees and gorillas differ in a number of other attributes (e.g., size of home range, migration pattern, group size, adult sex ratio, sexual dimorphism in body size and weight) which may equally be responsible for the differences in vocal behavior.

The aim of the following chapter is twofold: First, we will evaluate the relationship between vocal behavior and social organization by considering a larger spectrum of primate species with grouping patterns similar to those of gorillas (*harem groups*) and chimpanzees (*fission-fusion*.) respectively. Second, one particular aspect of sex differences in vocal behavior - the use of loud calls - will be examined in more detail.

VOCAL BEHAVIOR AND ITS SOCIAL CORRELATES

Harem Groups

The term harem group refers to cohesive one-male breeding units with a small number of adult females (Vogel, 1975). Leader males may tolerate other males born within their group but are usually extremely aggressive towards extra-group males. Out of the 172 species listed by Smuts et al. (1986, Table A-1), 33 are living in one-male groups or show a

Table 2. Comparative data from primate species living in harem groups.

Species	Size of group	Adult sex ratio (M:F)	Migration pattern	Loud calls	Home range (km ²)	Sex dimorphism index of body weight (F/M)	References
<i>Callimico goeldii</i>	6-9	1:2	?	yes	0.3-0.6	0.82	1, 1, -, 2, 1, 3
<i>Cebus capucinus</i>	11-20	1:5	M&F	yes	0.5-0.8	0.71	4, 4, 4, 5, 4, 3
<i>Alouatta seniculus</i>	4-10	1:1.6	M&F	M&F	0.04-0.25	0.79	6, 6, 7, 8, 6, 3
<i>caraya</i>	7-9	1:2	?	yes	?	0.85	6, 6, -, 9, -, 3
<i>Cercopithecus nictitans</i>	13-20	?	M	M	0.6-0.8	0.63	10, -, 11, 12, 13, 3
<i>mitis</i>	10-45	?	M	M	0.4-0.6	0.57	10, -, 11, 12, 13, 3
<i>diana</i>	14-40	1:7	M	M	1	0.62	10, 14, 11, 12, 13, 15
<i>cephus</i>	8-15	?	M	M	0.1-2.8	0.70	10, -, 11, 12, 13, 3
<i>campbelli</i>	8-13	?	M	M	0.4	1.00	10, -, 11, 12, 13, 3
<i>ascanius</i>	17-40	?	M	M	0.2	0.69	10, -, 11, 12, 13, 3
<i>Erythrocebus patas</i>	5-35	1:10	M	?	20-30	0.56	10, 16, 11, -, 16, 3
<i>Papio sphinx</i>	20-25	1:5	M	yes	5	0.46	17, 17, 11, 18, 19, 3
<i>hamadryas</i>	2-23	1:3	F	?	?	0.43	17, 17, 11, -, -, 3
<i>Theropithecus gelada</i>	10	1:3	M	?	?	0.66	17, 17, 11, -, -, 3
<i>Colobus guereza</i>	12	1:1.3	M	M	0.02	0.78	20, 20, 11, 21, 20, 3
<i>verus</i>	8	?	?	M	0.26	0.94	20, -, -, 14, 14, 3
<i>satanas</i>	15	1:2.6	M	M	?	0.79	22, 22, 11, 21, 22, 3
<i>polykomos</i>	16	?	?	M	0.17	0.81	23, 23, -, 21, 15, 3
<i>Nasalis larvatus</i>	9	1:3.6	M&F	M	0.8	0.48	24, 24, 24, 25, 24, 3
<i>concolor</i>	3-5	1:1.6	?	M	0.2-0.3	?	26, 26, -, 27, 26, 3
<i>Presbytis thomasi</i>	3-12	1:3	M	M	0.1-0.2	?	28, 28, 28, 28, 28, 3
<i>senex</i>	7-9	1:4	M&F	M	0.2-0.7	0.91	29, 29, 30, 31, 29, 3
<i>pileata</i>	4-13	1:4	M&F	M	0.14-0.22	0.90	32, 32, 32, 32, 32, 33
<i>johnii</i>	8-16	1:2.8	M&F	M	0.06	0.81	34, 34, 35, 36, 37, 3
<i>christata</i>	32	1:12	M	M	0.2	0.94	38, 38, 11, 38, 38, 3
<i>aygula</i>	3-12	1:2.7	?	M	0.1-0.4	0.98	39, 39, -, 39, 39, 3
<i>melalophus</i>	9-15	1:8	M	M	?	0.98	40, 40, 11, 41, -, 3
<i>Rhinopithecus roxellanae</i>	?	?	?	M&F	?	0.49	-, -, -, 42, -, 42
<i>Gorilla gorilla</i>	5-37	1:2.4	M&F	M	5-35	0.58	43, 43, 44, 45, 43, 3

grouping pattern similar to that of gorillas (small groups with a single or few adult males). The search for features common to all or most of these species demonstrates a remarkable incoherence (Table 2): In 20 species, loud calls are thought to be given exclusively by adult males but in 2 other species loud calls are given by both sexes. In the species grouped in this category all different types of migration patterns are practiced. Group size and home range size varies greatly and the degree of sexual dimorphism ranges from moderate (e.g., *Cercopithecus cephus*, *Presbytis aygula*) to extensive (e.g., *Papio hamadryas*). A previous review (Gautier and Gautier, 1977) identified 18 species in which loud calls (type 1) are given exclusively by adult males. Nine of these species are reported to live in one-male groups, seven in multi-male groups and one is probably monogamous (grouping patterns are from Smuts et al., 1986, Table A-1). In sum, there is little evidence that sex differences in loud call behaviour can be related to a particular type of social organization or grouping pattern. Instead, species showing similarities in vocal behavior differ with respect to other aspects of their social life and vice versa.

Fission-Fusion Society

The fission-fusion society is a rare social pattern among primates. Besides chimpanzees, the only other species with a similar social design are bonobos and the spider monkeys *Brachyteles* and *Ateles* (Table 3).

Pan: The grouping patterns of the two *Pan* species are more or less identical (Wrangham, 1986). Communities split into temporarily stable parties of differing size and composition. In contrast to chimpanzees, bonobos more often form bisexual parties and the number of adult males per party is higher. Female bonobos form unisexual coalitions, male bonding is comparatively weak and dominance relationships between the sexes are biased in favor of females (Nishida and Hiraiwa-Hasegawa, 1986; Parish, in press; White, 1988). Females participate actively during community encounters and occasionally gang up against adult males of their own community (personal observation). Mating occurs during the entire sexual cycle and involves most or all males. However, observations from Wamba and Lomako suggest that males of the same community mate at different rates (Kano, 1992; personal observation). Chimpanzees and bonobos are thought to vocally advertise the discovery of an abundant food patch (Wrangham, 1977; personal observation). Sex differences in vocal behavior appear minor. In chimpanzees, differences are most prominent in the rate animals of different age and sex use the different elements of the vocal repertoire (Marler, 1976). Preliminary analyses of vocalizations of bonobos recorded at Lomako

Table 2: M, male; F, female; yes, species has been reported to give loud calls but information on sex differences is not available; ?, no information available. The index of sex dimorphism was calculated by dividing the weight of females (in kg) by the weight of males using the data in the according references. References for each respective column are cited in the final column.

References of Table 2: 1, Goldizen (1986); 2, Masataka (1982); 3, Harvey et al. (1986); 4, Robinson and Janson (1986); 5, Oppenheimer (1977); 6, Crockett and Eisenberg (1986); 7, Sekulic (1982b); 8, Sekulic (1983); 9, Thorington et al. (1984); 10, Cords (1986); 11, Smuts et al. (1986, Tab. A-1); 12, Gautier (1988); 13, Gautier-Hion (1988); 14, Oates and Whitesides (1990); 15, Galat and Galat-Luong (1982); 16, Chism and Rowell (1988); 17, Stambach (1986); 18, Kudo (1987); 19, Hoshino et al. (1984); 20, Dunbar (1986); 21, Oates and Trocco (1983); 22, McKey and Waterman (1982); 23, Galat and Galat-Luong (1985); 24, Bennet and Sebastian (1988); 25, Kawabe and Mano (1972); 26, Watanabe (1981); 27, Tenaza (1989); 28, Gurmaya (1986); 29, Rudran (1973); 30, Manley (1986); 31, Hohmann (1990); 32, Stanford (1991); 33, Napier and Napier (1970); 34, Hohmann (1989a); 35, Moore and Ali (1984); 36, Horwich (1976); 37, Horwich (1972); 38, Bernstein (1968); 39, Ruhiyat (1983); 40, Struhsaker and Leyland (1986); 41, Wilson and Wilson (1975); 42, Tenaza et al. (1988); 43, Stewart and Harcourt (1986); 44, Harcourt (1978); 45, Schaller (1963).

suggest sex-related (and perhaps context-related) spectral differences in high hoots (Hohmann and Fruth, in press).

Brachyteles: Data obtained from habituated groups at two study sites have revealed contradictory results about the nature of social organization. Cross-sectional data from one site covering a period of nine years demonstrate an ample degree of variation (Strier et al., 1993): During the first six years, the study group remained comparatively cohesive. Occasional fission into smaller subgroups occurred and was correlated with increasing rates of contact calls between the dispersed group members. However, these fissions were restricted to short periods of time. It was only later that the group showed a regular pattern of fission-fusion into two subgroups of variable size and composition. At the other study site, fission-fusion occurs regularly and resembles that reported from chimpanzees (Milton, 1984). Here, reunions between group members involved antagonistic displays, loud calls and ritualized greeting (embracing). The latter occurred among females and among males but not between the sexes. Males were apparently dominant over females and formed alliances during agonistic interactions. Observations of mating behavior indicated that females mate with several male group members within short succession and even with males from a neighboring group (Milton, 1985). A repertoire of eight different calls has been described and the only reported sex difference in vocal behavior concerns the use of the *mating twitter*, a call given exclusively by females to attract males (Milton, 1984).

Ateles: Several members of this genus (e.g., *A. belzebuth*, *A. paniscus*) have been reported to live in fission-fusion societies (Klein and Klein, 1977; Symington, 1990). Groups split regularly into subgroups of flexible size and composition. Data on agonistic interactions indicate that both sexes engage in unisexual coalitions and males always dominate females. Agonistic intra-group interactions from males against females are rare or absent and male-male aggression involves predominantly or exclusively individuals from different groups. Females participate in agonistic interactions during inter-group encounters but are less active if male group mates are involved. As in *Brachyteles* tolerance among male group members is very high and in *A. paniscus* average association indices were highest for male-male dyads (Symington, 1990). Estrous females may be consorted by a single male but have also been seen to copulate repeatedly with a larger number of mates. In one species (*A. Geoffroyi*) males and females have been reported to give food calls in order to attract distant community members and manipulate the size of feeding parties (Chapman and Lefebvre, 1990). Males and females of *A. Geoffroyi* use the same repertoire of agonistic (*ook ook*, *growling*) and non-agonistic (*whoop*, *heavy panting*) distance calls (Klein, 1974). Eisenberg (1976) who studied vocal communication in two other species (*A. belzebuth*, *A. fusciceps*) has reported a very low degree of sex differences in vocal behavior. Two types of loud calls were distinguished and from the corresponding descriptions it is inferred that one was preferably used for intergroup communication while the other was given during interactions among group members.

There are a number of striking parallels among all those species living in a fission-fusion society. Most important for the present paper, loud calls are habitually given by females and males alike, some species having different signals for distance communication, and loud calls are used for both intra- and inter-group communication. Correspondence among the species living in fission-fusion societies is not restricted to the spatial distribution of group members but also includes other factors such as the adult sex ratio, the mode of migration and the degree of sexual dimorphism (Table 3). Thus, one could hypothesize that instead of being related to the fission-fusion society, the existence (or absence) of female loud calls is perhaps related to one of these other traits.

Table 3. Comparative data from primates species living in fission-fusion societies

Species	Size of group / community	Adult sex ratio M:F	Mean party size	Migration pattern	Loud calls	Size of home range (km ²)	Index of sex dimorphism in body weight (F/M)	References
<i>Pan troglodytes</i>	19-106	1:1.4	2.6-8.6	F	F&M	5-300	0.74	1,2,1,2,3,2,1,4
<i>paniscus</i>	50-120	1:2.1	7.6-16.8	F	F&M	22-60	0.74	1,5,1,1,3,6,1,7
<i>Brachyteles arachnoides</i>	22-25	1:1.2	?	F	F&M	0.7-1.7	1.00	8,8,-,9,3,9,10,4
<i>Ateles belzebuth</i>	18	1:2.9	3.5	F	F&M	0.3-0.4	0.93	8,8,11,12,3,12,13,4
<i>paniscus</i>	18	1:2.6	3.7-5.0	F	F&M	1.5-3.3	0.87	8,8,14,14,3,15,13,4
<i>geoffroyi</i>	15	?	?	F	F&M	0.1-1.2	0.93	8,-,-,-3,15,13,4

References: 1, Wrangham (1986); 2, Goodall (1986); 3, Smuts et al. (1986, Tab.A-I); 4, Harvey et al. (1986); 5, Fruth and Hohmann (in press); 6, Hohmann and Fruth (in press); 7, Jungers and Susman (1984); 8, Robinson and Janson (1986); 9, Milton (1984); 10, Strier (1987); 11, Klein and Klein (1975); 12, Klein (1974); 13, Symington (1990); 14, Symington (1988); 15, Eisenberg (1976).

While the pattern of fission-fusion is confined to a few species from two different taxons, the trait in question (female loud calls) is not. Although the number of species in which females give loud calls on a regular basis is restricted, it includes members of very different taxonomical groups (Table 4). Group structures and mating patterns are variable and include monogamous pairs, polygynous one-male groups as well as promiscuous multi-male groups and fission-fusion societies.

Rather than forming a uniform category, the samples of female loud calls pooled in Table 4 differ along several lines. (1) Physical structure: Loud calls of males and females may be monomorphic or dimorphic. (2) Mode of emission: Individuals of both sexes may vocalize simultaneously or independently of each other. If both sexes vocalize in unison, the calls given by different individuals may be superimposed on each other (chorusing) or males and females may alternate their vocalizations (duetting). (3) Time of utterance: Loud calls may be given at particular times (usually at dawn) or at any time of the day (or night). Along with field reports about the context of vocalization, these differences suggest that female loud calls may serve various functions. Behavioral observations and playback experiments have shown that female gibbons and howler monkeys give loud calls in order to aid exclusion of extragroup females (Raemaekers and Raemaekers, 1985; Sekulic, 1982a, b).

Female howlers interfere with loud calls when female group mates try to approach the dominant male and threaten subdominant females who try to howl together with the male (Sekulic, 1983). Parties of female spider monkeys encountering strange males respond with vocal bouts (ook-barking, whooping) lasting for periods as long as one hour (Klein, 1974). These and other examples (for corresponding data from *Aotus*, *Callicebus* and *Pithecia* see Robinson et al., 1986) suggest that female loud calls may facilitate defense of communal resources and intrasexual competition.

Vocal responses of female howlers towards the roaring of male group mates have been found to vary in relation to their reproductive status. It was suggested that howling by females in unison with their mates may enforce pair bonding and that affiliation with females in turn may strongly affect the male's ability to remain dominant (Sekulic, 1982a, 1983; Sekulic and Chivers, 1986). In chimpanzees the rate of pant hooting by females increases at the time of estrous (Pusey, 1990) and when travelling together with adult males in mixed parties (Clark, 1991). Thus, female loud calls may also advertise the reproductive state of the vocalizer and attract potential mates.

In bonobos, members of different female parties give high hoots spontaneously before or at the onset of locomotion. Individual parties may stay apart but remain in auditory contact for the entire day until they fuse at the nest site at night. The coincidence between onset of locomotion and distance vocalization indicates that high hoots maintain contact and coordinate travel routes between members of different parties (personal observation).

In conclusion, the use of loud calls by females is neither related to a particular type of social organization nor to a single function. In general, females seem to give loud calls for the same reasons as males (e.g., spatial regulation within and between groups, mate attraction, self-advertisement, intrasexual competition). Regarding function, loud calls are thought to facilitate communication between members of different groups. In addition, it is conceivable that loud calls are directed towards those individuals who are most likely to transfer between groups. If this is correct, one would expect to find a correlation between the mode of migration and sex differences in the use of loud calls. In most of the species (72%) listed in the according section (loud call type-1) by Gautier and Gautier (1977) adult males are the primary producers of loud calls, migration is male-biased or restricted to males. In contrast, Table 4 shows that in all species where females are known to give loud calls, migration is female-biased or both sexes migrate. It is therefore hypothesized that the

Table 4. Species in which loud calls are given by males and females.

Species	Migration pattern	Sex dimorphism (F/M)	Grouping pattern	Reference for vocalizations
<i>Alouatta</i>				
<i>palliata</i>	F&M	0.79	Sm-V	Baldwin & Baldwin, 1976
<i>seniculus</i>	F&M	0.77	Lg-M	Sekulic, 1982a
<i>pigra</i>	?	?	Sm-V	Horwich & Gebhard, 1983
<i>Ateles</i>				
<i>belzebuth</i>	F	0.94	C-i	Klein, 1974
<i>fusciceps</i>	?	1.02	C-i	Eisenberg, 1976
<i>geoffroyi</i>	F	0.94	C-i	Eisenberg, 1976
<i>Brachyteles</i>				
<i>arachnoides</i>	F	1.0	C-i / Lg-M	Milton, 1984
<i>Lagothrix</i>				
<i>lagotricha</i>	?	0.85	Lg-M	Williams, 1967
<i>Aotus</i>				
<i>trivirgatus</i>	F&M	1.09	Mon	Robinson et al., 1986
<i>Callicebus</i>				
<i>moloch</i>	F&M	0.95	Mon	Robinson et al., 1986
<i>torquatus</i>	F&M	1.00	Mon	Robinson et al., 1986
<i>Pithecia</i>				
<i>monachus</i>	F&M	?	Mon	Robinson et al., 1986
<i>pithecia</i>	F&M	0.88	Mon	Robinson et al., 1986
<i>Presbytis</i>				
<i>potenziani</i>	F&M	0.98	Mon	Tilson & Tenaza, 1976
<i>Hylobates</i>				
<i>agilis</i>	F&M	0.95	Mon	Gittins, 1980
<i>concolor</i>	F&M	1.04	Mon	Deputte, 1982
<i>hoolock</i>	F&M	0.94	Mon	Tilson, 1979
<i>klossii</i>	F&M	1.04	Mon	Tenaza, 1976
<i>lar</i>	F&M	0.93	Mon	Carpenter, 1940
<i>moloch</i>	F&M	0.95	Mon	Kappeler, 1984
<i>muelleri</i>	F&M	?	Mon	Mitani, 1984
<i>pileatus</i>	F&M	?	Mon	Srikosamatara, 1980
<i>syndactylus</i>	F&M	0.97	Mon	Chivers, 1974
<i>Pan</i>				
<i>trogodytes</i>	F	0.75	C-i	Goodall, 1968
<i>paniscus</i>	F	0.74	C-i	Hohmann & Fruth, in press

Grouping patterns and data on migration for species living in groups (communities) with more than one female were taken from Smuts et al., 1986, Tab. A-I. The index of sex dimorphism was calculated by using the data on body weight (kg) of males and females published by Harvey et al., 1986, and Jungers and Susman, 1984 (for *Pan paniscus*), respectively.

positive correlation between the two traits, female-biased migration and female loud calling, indicates a functional linkage.

We are aware that there are limitations to the concept developed above. First, it is not clear why in some species with female-biased migration, neither sex uses loud calls (e.g., *Macaca radiata*, Hohmann, 1989b; *Colobus badius*, Struhsaker, 1975). Second, members of the phylopatric sex may not always refrain from giving loud calls (e.g., male chimpanzees and bonobos). Third, there is apparently no species where loud calls are given exclusively by females. The only species coming close to that is the silver gibbon (*Hylobates moloch*) where females rather than males give loud calls (Kappeler, 1984). Finally, there are species where males give loud calls but females, in spite of their tendency towards exogamy, do not (e.g., *Nasalis larvatus*, *Gorilla gorilla*).

In gorillas, both sexes migrate but loud calling is thought to be restricted to adult males. However, Fossey (1972) indicates that there are exceptions from this rule. She reports two cases where hoot series were given once by an adult female and once by a juvenile of unknown sex. No contextual information is provided except that at the time of observation the female was a member of an all male band. Though these exceptional cases may justify changing the status of the behavior from "absent" to "rare", they do not diminish the overwhelming sex bias in loud calling of gorillas. Are there any alternative explanations why female gorillas refrain from producing loud calls?

Gorillas subsist on an evenly dispersed folivorous diet, they are not territorial and females may gain little (if any) nutritional benefits from migration (Watts, 1985). Instead, female gorillas seem to be associated with silverback males in order to receive protection against predators (Harcourt et al., 1981). There is probably little difference for the females whether a silverback extends his protection towards two or towards three of them. In contrast to nutritional resources, male protection could be considered a divisible resource. One could speculate that female gorillas refrain from loud calling because of the low degree of intrasexual competition. However, recent analyses of the distribution of aggressive behavior between female group members indicate high rates of social conflicts between long-term residents and recent immigrants (Watts, 1994).

Another factor not yet considered here is sexual dimorphism in body size and weight. One of the driving forces for sexual dimorphism is intra-sexual selection (Darwin, 1871). There is evidence that certain acoustical parameters of primate calls vary with body size (Gautier-Hion and Gautier, 1985; Hauser, 1993; Inoue, 1988). Assuming that judgements of the fighting abilities of potential opponents are based on vocal cues, weaker males would have no advantage from loud calling. Vocalizing in unison with other group members would be an alternative strategy because chorusing of males and females would probably prevent distant listeners from evaluating body size (and fighting ability) of opponents. With the support of many females, smaller males could be more successful than large males. It is obvious that such a trend would either inflate the value of the signal or decrease sexual dimorphism. Table 4 shows that in all species where females give loud calls and migrate, sexual dimorphism is indeed relatively low. In contrast, for those species where this correlation does not apply (e.g., gorilla, proboscis monkey, hamadryas) the indices for sexual dimorphism are exceptionally high (Harvey et al., 1986). However, Table 2 shows that in some species (e.g., *Colobus*, *Presbytis*) where both attributes, loud calling and migration, are thought to be a domain of males, sexual dimorphism can be very low. Hence, the relationship between sexual dimorphism and sex differences in the use of loud calls is inconsistent.

Suggestions for future studies: We are just beginning to understand vocal communication in the great apes and some of the noted examples indicate an unexpected capacity for natural communication. However, there are still large gaps in our knowledge.

For example, mountain gorillas have been studied for several decades but even the most basic aspects of their distance communication remain unexplored. Similarly, individual chimpanzees were monitored by researchers for their entire lives but the ontogeny of vocal communication is unknown. Finally, field studies on bonobos are less comprehensive than those on chimpanzees. If we are to understand the development of vocal communication, we must be able to compare patterns of all the great apes in light of their respective physical, ecological and social constraints. There are a number of recommendations for future research in this area (e.g., Boehm, 1989; Seyfarth, 1986) and the recent studies on chimpanzees can also serve as examples for corresponding studies on other species. However, what is required are more comprehensive field studies. For example, one of the issues raised in this chapter - the function of sex differences in loud call behavior - can be approached in different ways:

(1) Playback experiments: In some species (e.g., gibbons) the degree of sex differences of loud calls has been well documented. In other species (e.g., chimpanzees, howlers, spider monkeys) the degree of sex differences is not known and analyses of the structural features are required. Playback experiments (similar to those conducted by Raemaeker and Raemaeker, 1985) could be used to evaluate the response of males and females to loud calls from both sexes.

(2) Analysis of the context of loud calling: At which age do females and males begin to give loud calls and what social conditions lead to habitual use of this behavior? For example, there may be a link between sexual maturity and loud call production (e.g., Gautier and Gautier, 1977). However, observations on some species indicate that this is not simply an age phenomenon but a social one. Male gibbons and langurs refrain from loud calling until they have established their own territory and are again accompanied by females (Hohmann and Vogl, 1991; Tenaza, 1976). Therefore, to evaluate the significance on female loud call performance, the vocal activity of individuals must be known in a number of contexts such as before, during and after migration.

(3) Relationship between vocalization and group dynamics: If loud call behavior of resident group members transmits information on the size and composition of the group and can act to attract or repel migrating conspecifics, one would expect the rate of vocalization, group size, rate of visits of potential migrants and actual rate of immigration to be correlated. Long term studies on well habituated groups or communities are required to collect this kind of data.

(4) Effect of group transfer: If loud calls of males and females are used to regulate migration (e.g., attract members of the opposite sex and/or repel individuals of the same sex), how is migration regulated in species in which the migrating sex (or both sexes) does not produce loud calls? Differences in vocal behavior (presence/absence of loud calls) could be related to the total density of primates in a particular area, the degree of interspecific food competition or the presence of predators.

Finally, there is a very simple way to enhance our understanding of sex differences in loud call behavior: When recording calls, do not automatically score vocalizations as a "male loud call" but try to determine the sex and identity of the caller. As additional data on sex differences in the use of loud calls become available it will be then possible to examine in greater detail the social and ecological conditions under which female primates raised their voices.

CONCLUSIONS

All species of great apes utter loud calls which correspond in a number of structural and behavioral patterns. They are always given in phrases consisting of more or less distinct

sections, and are often combined with acoustical cues. Loud calls are regularly given by adult males and in those species where relevant data are available, dominant individuals vocalized more often than subdominants. Concerning the use of these calls, species-specific differences are more prominent than common features. In two species (orangutan and gorilla), vocalization is restricted to adult males and behavioral observations and field experiments suggest that spacing among single males or members of different groups is the major function.

In chimpanzees and bonobos, loud calls are used by mature and immature individuals of both sexes and play a major role in communication between members of the same community. Structural features vary with differences in rank, context of emission, and specific functions. Sudden changes of individual-specific features indicate a high degree of flexibility in physical traits.

Comparison of a larger set of species does not support previous propositions concerning an interrelation between type of social organization (grouping pattern) and sex differences in utilization of loud calls. Instead, cross-species comparison suggests a positive correlation between migration patterns and use of loud calls: In species in which migration is male-biased or restricted to males, loud calls are given exclusively (or predominantly) by males. In species in which migration is female-biased or both sexes migrate, loud calls are given by both sexes. These findings are in general agreement with previous hypotheses concerning the functional significance of loud calls. However, the fact that some species do not follow this trend demonstrates the need for additional research.

ACKNOWLEDGEMENT

The authors thank Irenäus Eibl-Eibesfeldt, Gerhard Neuweiler and Detlev Ploog for continuous support. Excellent comments on an earlier version by Elke Zimmermann, Marc Hauser and Bertrande Deputte are gratefully acknowledged. Special thanks are due to Christopher Roberts and Tom Van 't Hof for valuable recommendations, critical reading and corrections of the English text. Financial support for the field-work in Zaire was provided by the Max-Planck-Society, the University of Munich, the German Science Foundation, the German Academic Exchange Service, and a private donor.

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