

RESEARCH ARTICLES

Rank Differences in the Production of Vocalizations by Wild Chimpanzees as a Function of Social Context

ADAM P. CLARK

Department of Anthropology, University of Michigan, Ann Arbor

Rank differences in the production of vocalizations by wild, semihabituated, unprovisioned chimpanzees were investigated during a 10-month study in the Kibale Forest, Uganda. Vocalization rates were calculated from data collected during 230 hours of focal-animal sampling on adult females, adult males, and subadult males. Rates were calculated according to whether individuals were alone, with adult females only, or in mixed parties, and the results were compared with published data collected at the Gombe provisioning area. Adult females and low-ranking adult and subadult males were generally quiet except when they were in mixed parties, whereas high-ranking males vocalized in all social contexts. These results were in partial contrast to data collected at Gombe, which indicated that vocal production was similar across all age and sex classes. Vocal production at Gombe did, however, resemble that from mixed parties at Kibale, suggesting that the provisioning area at Gombe was comparable to a natural socioecological context occurring at large fruiting trees. It is suggested that low-ranking chimpanzees refrain from loud vocalizing when they are alone or with females only in order to avoid attracting feeding competition and/or potentially aggressive males. These individuals may vocalize when they are associating with high-ranking males in order to advertise the presence of large parties and to deter other individuals from joining them. The use of loud, interparty calls by high-ranking males, when alone or with others, is consistent with the greater sociality of adult male chimpanzees. Loud calling might be advantageous for adult males in attracting mates or allies. © 1993 Wiley-Liss, Inc.

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INTRODUCTION

Because social interactions depend greatly on communication, the nature of social relationships within groups is likely to influence the patterning of primate vocal behavior [Marler, 1976]. Numerous studies have shown that the structure and patterning of primate vocal signals can vary with subtle changes in ongoing social context, revealing previously unsuspected flexibility in primate vocal communication [Snowdon & Cleveland, 1984; Biben & Symmes, 1986; Biben et al.,

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Address reprint requests to Dr. Adam P. Clark, 135 Puhalka Road, Newfield, NY 14867.

1986; Symmes & Biben, 1988]. Vocalizations from several primate species appear to function in a representational fashion within the social domain [Gouzoules et al., 1984; Masataka, 1986; Gouzoules & Gouzoules, 1989]. The presence of specific individuals is known to affect the production of calls by group members [deWaal, 1982; Cheney & Seyfarth, 1985; Goodall, 1986; McConnell & Snowdon, 1986; Hauser, 1991], and the recent history of social interactions with familiar individuals may affect individual perceptual responses [Snowdon, 1988]. Yet while it is clear that vocal signaling can be extremely sensitive to social context, relatively little attention has been given to the role that fundamental relationships within primate groups (e.g., sex-linked patterns of affiliation or agonism) might play in shaping patterns of vocal behavior. This gap is significant because the nature of social relationships within primate groups may have played an important role in the evolution of complex vocal communication.

In two recent studies it was concluded that within-group social dynamics, but not species social structure, influenced the use and structure of primate calls. In a study comparing two macaque (*Macaca silensis* and *M. radiata*) and two langur species (*Presbitis johnii* and *P. entellus*), Hohmann [1991] found that the use of closely related calls was similar within genera, despite differences in overall social structure (one-male vs. multi-male) and habitat specialization (arboreal forest vs. flexible semiterrestrial adaptations). He suggested that minor interspecific differences within genera were instead a consequence of specific patterns of individual interactions (related, for example, to group cohesion or mating behavior). Gouzoules and Gouzoules [1989] found that the screams used by pigtail macaques (*M. nemestrina*) in the recruitment of aid during agonistic encounters differed in acoustic morphology from those used by rhesus macaques (*M. mullata*) [Gouzoules et al., 1984] in identical contexts. Pigtail and rhesus macaques both live in large, usually multi-male groups [Melnick & Pearl, 1987]. Gouzoules and Gouzoules [1989] suggested that acoustic differences in scream vocalizations between the two species were due to differences in the relative importance of matrilineal relatedness in agonistic alliances.

In a previous quantitative study comparing female and male chimpanzee call usage in the wild, Marler [1969, 1976; Marler & Tenaza, 1977] found that (1) the average number of vocalizations (vocalization type not considered) uttered by individuals of each age/sex class was nearly identical, and (2) the production of all chimpanzee vocalization types was shared by all age and sex classes. Marler [1976] concluded that fission/fusion social organization placed similar demands on all individuals within the community, and selected for relatively similar patterns of vocal production among the age and sex classes. In this view, features of group life, in particular patterns of dispersion and aggregation, were seen to affect all individuals more or less equally, and to overshadow social relationships within the group in determining patterns of vocal production.

However, this study of wild chimpanzee vocal production was based on observations made exclusively at the Gombe provisioning station [Marler, 1969]. Using camp records, Wrangham [1974] found that average party size increased with provisioning at Gombe, and that the frequency of aggression increased with party size. Thus Marler's data were probably biased toward large and highly excited aggregations, as he himself noted [Marler, 1976].

Long-term studies of chimpanzees in the wild have consistently reported the extremely labile nature of chimpanzee subgroups [Goodall, 1965, 1986; Nishida, 1968, 1990]. These studies have further indicated that relationships between males, between males and females, and between females differ greatly [see also Clark, 1991, and Wrangham et al., 1992, for analyses of behavioral data from

Kibale Forest, where patterns of social relationships generally similar to those reported from the Tanzanian study sites appear to exist]. Ranging patterns of males and females are also known to differ [Wrangham, 1979b; Wrangham & Smuts, 1980; Hasegawa, 1990]. In view of these observations, it is therefore possible that individual differences in vocal production were masked in the Gombe provisioning area due to the predictable presence of food and large aggregations of individuals. In this paper I provide data to determine if rank, which is largely determined by age and sex [Bygott, 1979], and the composition of temporary subgroups affect patterns of vocal production in habituated but unprovisioned chimpanzees of the Kibale Forest. Elucidating these patterns will constitute an initial step toward describing the social foundations of vocal complexity in chimpanzees.

METHODS

Observation of the Kanyawara Study Group

The research reported here was carried out between February and December, 1989, in the Kanyawara study area of the Makerere University Biological Field Station (MUBFS), located in the north-central part of the Kibale Forest Reserve, Toro district, western Uganda. Detailed descriptions of Kibale Forest may be found in Kingston [1967], Wing and Buss [1970], Struhsaker [1975], Ghiglieri [1984], and Skorupa [1988]. Descriptions of the Kanyawara study area and the study community may be found in Clark [1991], Wrangham et al. [1992], and Clark and Wrangham [1993].

The majority of observations were made while the chimpanzees were in fruiting trees (roughly 70%). An observation session was defined as a continuous period spent with a subgroup, or party, of chimpanzees in which the composition of the party may have changed partly but not entirely (see below for working definitions of a party). Chimpanzees were located for observation sessions by a variety of methods. The most effective method was visiting fruiting trees where chimpanzees had already been observed feeding (56 times). In general I arrived at preferred fruiting trees before dawn in order to monitor as many arrivals as possible. When many trees attractive to the chimpanzees were in fruit, subjects were sometimes located by following calls (20 times). Once I followed parties until they nested for the night, permitting resumption of observation at the night nest the following morning. Animals were also discovered once by chance observation while I walked through the study area.

Observation sessions were terminated in a number of ways. Most frequently I lost the chimpanzees when they traveled faster than I was able to follow through dense undergrowth (53 times). Less frequently I abandoned observation when one of the following situations held: (1) I was unable to target any individual for at least 1 hour (6 times); (2) while observing the chimpanzees, I chose a termination time 1 hour in advance due to fatigue (5 times); (3) a 1- or 2-hour observation session was scheduled before contacting the chimpanzees, beginning with the first target of the day (3 times); (4) a termination time was chosen prior to locating the chimpanzees for the day (10 times); (5) the chimpanzees made their night nests (once); or (6) observation ended abruptly when the chimpanzees were alarmed by human activity (once).

Defining a Party Under Observation

A party was defined as one or more individuals traveling, feeding, resting, or socializing within 50 m of one another. In practice parties were usually easy to identify since individuals tended to cluster in close proximity (e.g., in the same tree feeding, or within a few meters of one another during grooming bouts). In addition,

since most trails were spaced 50 m apart in the gridded trail system, it was possible to quickly monitor the areas surrounding parties under observation. Nonetheless, it was not always possible to be certain whether unseen individuals were in close proximity (i.e., within 50 m), especially during travel. In these cases individuals were scored as being in the same party if they left one location at the same time and arrived at a new one within 15 minutes of each other, even if they were not simultaneously in view in the interim and some had been out of view for greater than 15 minutes. If individuals arrived at a new location successively over a period of time, they were considered to be in the same party if not more than 15 minutes lapsed between any two successive arrivals. If an individual departed from one location with a party but was not observed again, it was considered absent from the time it was last observed.

The identities of all individuals in the target animal's party were recorded as soon as possible after the beginning of an observation session, and changes in party composition were noted as they occurred.

Focal-Animal Sampling

Focal-animal sampling [Altmann, 1974] was used to determine individual rates of vocal production. Sampling began as soon as individuals came into view, and all individuals were about equally visible during focal animal sampling.

Four classes of individuals were distinguished for analysis based primarily on relative rank: adult female with or without dependent offspring (AF), subadult male (SAM), low-ranking adult male (AM2), and high-ranking adult male (AM1). The relative dominance ranks of males were determined by the outcomes of social interactions involving grunts and displacements recorded ad lib [Altmann, 1974] over the course of 565 observation hours [Clark, 1991]. Although not all of the adult males could be ranked in relation to each other, the following hierarchy was determined (from highest to lowest): ST = SY, TU, BF, BB, LB, LM, SL. Subadults were lower ranking than adults. Females and subadult males were all low-ranking, but were considered separately to determine if a sex difference existed in vocal behavior among low-ranking individuals. Individuals were assigned to age classes using the categories described by Goodall [1986, p. 81], based on visual assessments of physical and behavioral development.

Initial targets in an observation session were chosen on the basis of age/sex class first, and individual identity second, in the following order: adult male, adult female, subadult male, subadult female. For example, if I began with an adult female one day, then the following day I sought to begin with a subadult male. If no subadult male appeared, then I chose a subadult female, and so on. Within a class, an individual was chosen on the basis of how often it had been a target relative to other potential targets (i.e., new subjects were chosen over former subjects, and infrequently sampled individuals were chosen over others), and then on the basis of a fixed list of their names. After an initial target was chosen, subsequent targets in an observation session were chosen according to the same rotation criteria.

Individuals were observed as focal targets for 10 minutes at a time, with observations rotated among all adult and subadult individuals visible in a party. The different rank classes were sampled for roughly equal amounts of time. All analyses initially treated individuals separately.

Focal-animal sampling was possible for 233.8 of 360.2 (64.9%) observation hours on 86 parties of chimpanzees, resulting in the following distribution of 10-minute focal samples: 428 for anestrus adult females, 75 for estrus adult females, 393 for subadult males, and 530 for adult males. The total amount of time indi-

TABLE I. Adult and Subadult Kanyawara Chimpanzees as of December, 1989, With Amount of Time as Targets of Focal-Animal Sampling

Age/sex class ^a	Name ^b	ID	Age ^c	Target time (hrs)	Samples ^d
Adult female 1	Lope	(LP)	26	26.8	154 (0)
	Katono	(KO)	35	0	0 (0)
	Auntie Rose	(AR)	40	6.1	37 (0)
	Nyakagera	(NK)	26	0.8	5 (0)
	Teddy	(TD)	22	2.1	14 (0)
	Finger	(FG)	30	15.8	95 (37)
	Jennifa	(JA)	30	0.6	6 (0)
	Kabarole	(KL)	23	23.3	137 (0)
Adult female 2	Stump	(PU)	23	0.2	1 (0)
	Alice	(CE)	30	3.0	22 (14)
	Kyara	(KY)	35	1.5	8 (0)
Adult male 1	Sly	(YS)	26	3.6	24 (24)
	Stout	(ST)	33	17.0	111
	Stocky	(SY)	26	25.5	150
	Tofu	(TU)	30	2.4	17
Adult male 2	Badfoot	(BF)	24	19.6	126
	Big Brown	(BB)	23	3.4	22
	Light Brown	(LB)	20	11.5	69
	Lamy	(LM)	36	4.1	25
Subadult female	Slim	(SL)	18	1.5	10
	Jolly	(YJ)	13	2.2	13 (13)
Subadult male	Hippie	(FH)	12	0.0	0 (0)
	Yogi	(YB)	13	18.7	116
	Imoso	(MS)	11	8.7	55
	Johnny	(AJ)	13	15.3	95
	Rwenzori	(RZ)	11	10.3	66
	Julian	(NJ)	16	10.0	61
Total				233.8	1,439
% Total time focal observation possible ^e				67.6	

^aAdult females 1 and 2 = adult females with and without dependent offspring, respectively; adult males 1 and 2 = high- and low-ranking adult males, respectively.

^bIndividuals identified by name, with two-letter abbreviations used in the field. Most of the subjects were identified and named by G. Isabirye-Basuta, between 1983 and 1985. Note that JA and FG may be the same individual. Details in Clark [1991].

^cAll ages are estimates based on visual assessments of physical and behavioral characteristics, using as a guide Goodall's [1986, p. 81] description of the stages of the chimpanzee life cycle. Earlier assessments by Isabirye-Basuta (from his 1983-1985 study, personal communication) were also incorporated. Details in Clark [1991].

^dTotal number of times individual was a target of focal-animal sampling. For females, number in parentheses represents number of times when in estrus.

^ePercentage of total time following the animals in which it was possible to implement focal-animal sampling.

vidual chimpanzees were targets of focal-animal sampling is shown in Table I. Individuals observed for less than 1 hour were not included, so that a total of 230.1 focal hours are represented in the vocal production analysis.

Quantifying Vocal Production According to Social Context

To describe patterns of vocal behavior among Kibale chimpanzees, individual rates of call use were quantified for 11 vocalization types, or calls. Total vocalization rates were calculated for 21 known individuals. In addition, rates were calculated separately for three types of subgroups in which individuals were observed

feeding, resting, and traveling. The 11 vocalization types were subsequently divided into two broad functional classes, "submissive" and "nonsubmissive," to facilitate comparison between rank classes and party types. This division was based on Goodall's [1986] functional classification of chimpanzee vocalizations (see below). However, I emphasize that the division is crude, since it certainly obscures subtleties in ongoing emotional states associated with the social contexts in which the vocalizations occurred.

Vocalization categories used in this study. Vocalizations were initially assigned to 15 categories during field observations, and subsequently assigned to 11 categories for analysis (Table II). The categories were primarily based on Marler's [1976; Marler & Tenaza, 1977] catalog of chimpanzee vocalizations [acoustic descriptions may be found in Marler, 1969; Marler & Hobbett, 1975; Marler & Tenaza, 1977]. Discrimination in the field was based on regular reference to a tape recording of Gombe chimpanzee vocalizations made by Dr. M. Hauser from a film soundtrack [Marler & Lawick-Goodall, 1971], and to Goodall's [1968a,b; 1986] written descriptions of chimpanzee vocalizations and the contexts in which they occur. The following differences from Marler are shown in Table II: (1) I scored hoots separately from pant hoots if no climax phase occurred, although the two categories can be combined for comparative purposes; (2) as discussed below, I lumped for analysis a number of calls that were often difficult to distinguish in the field, i.e., (a) bark and waa-bark, (b) all soft food calls, and (c) all non-food-related grunts and pants; (3) following Goodall [1986], I distinguished hoos and whimpers (a whimper is a series of hoos, and therefore Marler and Tenaza lump them all as whimpers); and (4) also following Goodall [1986], I distinguished male and female copulatory calls. Three vocalizations were never heard during focal observations: nest grunt, laughter, and wraah. These calls were occasionally heard during ad lib observation sessions.

I used Marler's [1976] catalog, as opposed to Goodall's [1986] more extensive 32-call catalog (compared in Table II), because it was clear from the outset of the study that I could not distinguish consistently Goodall's finely discriminated, related call types under Kibale field conditions (e.g., different screams, or different grunts). Therefore broad, easily distinguished categories were used, which also meant lumping calls that commonly intergraded with one another, even though the extreme forms could be distinguished. For example, pants, grunts, and the combined pant-grunts are relatively easy to distinguish, and I scored them separately in the field. However, a submissive individual will frequently employ all three in an extended vocalization sequence, grading from one to the next without pause or obvious order, and merging type forms into ambiguous amalgamations. Consequently, analyzing such frequently intergraded calls separately would have overestimated my ability to distinguish them reliably under field conditions.

Lumping vocalization categories undoubtedly masked some of the complexity of the chimpanzees' vocal behavior. Nonetheless, broad differences, for example, in the use of submissive vocalizations, or in the use of vocalizations that broadcast individual identity and location over long distances, were probably preserved. More controlled conditions, and ultimately the use of playback experiments, will be necessary to detect the subtleties that may exist within groups of acoustically similar calls.

Functional classification of call types. No functional analyses (e.g., playback experiments) have yet been conducted for specific chimpanzee vocalizations. To interpret differences in overall vocal behavior, therefore, I grouped the 11 vocalization types into two relatively obvious functional classes: (1) Vocalizations

TABLE II. Vocalization Categories Used in This Study, Compared With Marler and Tenaza [1977] and Goodall [1986]

This study	Marler and Tenaza [1977]	Goodall [1986]	Context [Goodall, 1986] ^a
Pant hoot	Pant hoot	Roar pant hoot	Charges, stranger contact, social excitement
		Arrival pant hoot	Arrival at good food source, joining others
		Inquiring pant hoot	During travel, on high ridges
		Spontaneous pant hoot	During peaceful feeding, resting
Hoot ^b	(With "pant hoots")	(With "pant hoots")	
Bark	Bark	Bark	Social excitement, especially females
	Waa-bark	Waa-bark	Agonistic contexts, often by bystanders
Cough	Cough	Cough (or soft bark)	Mild threat given to lower ranking individuals
Hoo	Whimper	Hoo	Contact call, beg, especially mothers and infants
		Huu	Surprise, mild anxiety to unfamiliar objects
Food grunt	Grunt	Food grunt	Begin calm feeding on preferred food
	Rough grunt	Food aaa	Excited feeding, approaching preferred food
Copulation scream	(With "scream")	Copulation scream	Females during copulation
Whimper	Whimper	Whimper	Distress, especially infants (series of "hoos")
Squeak	Squeak	Squeak	Response to threat by dominant individual
Scream	Scream	Victim scream	While being attacked
		Tantrum scream	Weaning conflict, post-aggression frustration
		SOS scream (Copulation scream)	Appeal for help after attack
		Crying	Infant/juvenile combine whimper and tantrum scream
Grunt	Pant-grunt	Pant-grunt	Up hierarchy, reunions, social excitement
		Pant-bark	Up hierarchy, reunions, social excitement
		Pant-scream	Up hierarchy, reunions, social excitement
		Pant	Greeting, grooming
		Soft grunt	During foraging or traveling
Copulation pant ^c	(With "pant")	Extended grunt	Resting
		Copulation panting	Males during copulation
Nest grunt ^c	(With "grunt")	Nest grunt	Looking for nest site, making nest, settling in nest
Laughter ^c	Laughter	Laughter	During play
Wraah ^c	Wraah	Wraah	Alarm at dangerous creatures, bizarre behavior

^aAll of Goodall's [1986] contexts apply to the lumped categories used by Marler and Tenaza [1977] and this study. ^b"Hoots" and "pant hoots" were treated separately, since they are easily distinguished (hoots have no climax phase), but they can be readily combined for comparative purposes. See text for details about lumping categories. In general, my lumping does not reflect disbelief of a narrower category, but rather my inability to systematically discriminate intergraded calls under field conditions.

^c"Copulation pant," "nest grunt," "laughter," and "wraah" were not observed during focal observations.

typically given by lower ranking individuals during agonistic interactions with higher ranking individuals (here called "submissive" vocalizations). Following Bygott [1979, p. 407], agonistic interactions involved behaviors of aggression, flight and avoidance, submission, reassurance, and frustration. Vocalizations given during agonistic interactions were in general obviously directed at a specific individual, and elicited no vocal response. (2) Vocalizations typically given during vocal interactions in which more than one individual was vocalizing, or given in the absence of other vocalizations but without any other obvious behavioral interaction involving the vocalizer ("nonsubmissive" vocalizations). These vocalizations were often generally broadcast (exceptions were the hoo and cough, discussed below). The frequency of use of "submissive" vs. "nonsubmissive" vocalizations was compared between individuals in different party types to determine how the vocal behavior of different rank classes was affected by social context.

Of the 11 vocalization categories used in this analysis, Goodall [1986] describes 3 that are associated with social apprehension or fear: the squeak, the scream, and the pant-grunt (Table II). These vocalizations form the basis of the "submissive" vocalization group (with grunts including all non-food-related grunts, pants, and pant-grunts). A fourth vocalization, the whimper, frequently intergrades with squeaks and screams, and was therefore also included in the "submissive" vocalization group.

The remaining seven call types (pant hoot, hoot, bark, cough, hoo, food grunt, copulation scream) were designated as "nonsubmissive." Two of these calls share characteristics with the "submissive" vocalizations. The cough is usually directed at a specific individual and occurs in agonistic interactions, but is given by the higher ranking individual (e.g., often when a higher ranking individual supplants a lower ranking one). The hoo is also often directed, for example between mothers and offspring. However, it may be generally broadcast, and may occur in response to distant vocalizations or as part of a vocal exchange.

Data collection. All vocalizations uttered by a target animal were marked on a check sheet and, when possible, tape-recorded. Successive utterances of the same vocalization type (e.g., a sequence of screams without pause) were scored only once, following Marler [1976]. If a pause of at least 1 minute occurred, the vocalization was scored again. Two compound calls, the pant hoot (which includes hoes, hoots, and screamlike elements) and the whimper (which is comprised of a series of hoes), were scored as single vocalization types (i.e., their components were not scored). Vocalization rates were calculated for each individual as the total number of calls scored in the study divided by the total number of observation hours for that individual. Values for the four rank classes were subsequently calculated as averages of individual rates.

Although it is possible that some soft calls may have gone undetected during data collection, this was unlikely to have been a significant source of error. I used only focal-animal data from well-observed targets that were never more than 20 m away, and generally much closer (5–10 m). Most soft vocalizations are easily audible in this range. In addition, the most likely context for vocalizations to go undetected would be during periods of group excitement when many individuals are vocalizing and moving about. Yet it is in these very contexts that individuals tend to vocalize loudly.

Party types. Vocalization rates were calculated for each call for each individual in three different associations of individuals, and for all observations combined. The associations, or party types (see above for a definition of a party), were ones commonly observed in the field. They are defined as follows:

TABLE III. Mean Party Size for Two Party Types by Age/Sex Class*

Party type ^a	Age/sex class		
	AF	SAM	AM
PT2	4.9 ± 1.3 (106)	4.7 ± 2.5 (126)	3.8 ± 1.1 (86)
PT3	12.5 ± 6.2 (949)	11.9 ± 6.5 (1,006)	14.1 ± 5.6 (774)

*Values represent means ± standard deviations across ten-minute samples. Values in parentheses are number of ten-minute samples upon which means are based. AF, adult female; SAM, subadult male; AM, adult male; PT, party type (see text for details).

^aNote that the overall composition of a party type depends on the sex of the focal, so that the figures differ slightly for the different classes. For example, PT2 for an adult female focal contains no adult males, but for an adult male focal it contains one adult male (i.e., the focal).

Party Type 1 (PT1): Individual is “alone,” meaning that no other adults or subadults are present, but that infants and/or juveniles may be present.

Party Type 2 (PT2): Individual is with at least one adult female, with or without subadult females, infants, and/or juveniles, but without adult or subadult males;

Party Type 3 (PT3): Individual adult female is with at least one adult male, with or without subadults, juveniles, and/or infants; individual subadult male is with at least one adult male, with or without adult females, subadults, juveniles, and/or infants; individual adult male is with at least one adult male and one adult female, with or without others.

Infants and juveniles were included in Party Type 1 since all of the frequently observed females traveled with dependent offspring, and the inclusion of these individuals made it possible to compare adult females with solitary adult males. Mean party sizes for Party Types 2 and 3 are shown in Table III. Parties with more than one adult male and no adult females were rare (8 parties) and were not included in Party Type 3. Estrous females were not seen frequently enough during the study to determine their possible impact on calling behavior.

Analyses of Vocalization Rates by Party Type

Marler [1976] found that total vocal production rates were similar for all age and sex classes of chimpanzees at Gombe, and that all age and sex classes shared in the production of all vocalization types. To test these findings at Kibale, the following three analyses were performed.

First, mean vocalization rates for all calls combined, and for “submissive” and “nonsubmissive” calls, were computed for the four rank classes for all parties combined. This initial analysis was done in an effort to replicate Marler’s work under a broader range of observational conditions, as compared with observations made only in a provisioning area. As discussed above, if patterns of vocal behavior are influenced by social context, then differences in vocalization rates, and in the types of calls used, between the different classes of individuals are expected to emerge when the range of observational contexts is expanded.

TABLE IV. Rank Class Vocalization Rates for All Parties Combined: Total Rates, and Submissive and Nonsubmissive Rates Compared*

Rank class	Mean calls/hour			Observation hours (N)
	Submissive ^a	Nonsubmissive ^b	Total	
AF	1.9 ± 1.3	1.7 ± 1.3	3.6 ± 2.0	82.8 (8)
SAM	2.0 ± 0.8	1.6 ± 1.2	3.6 ± 2.0	63.0 (5)
AM2	0.4 ± 0.3	1.5 ± 0.8	1.9 ± 0.8	20.5 (4)
AM1	0.0 ± 0.0	3.9 ± 2.3	3.9 ± 2.3	64.5 (4)

*AF, adult female; SAM, subadult male; AM2, low-ranking adult male; AM1, high-ranking adult male; N, number of individuals the mean is based on.

^a"Submissive" calls include all non-food grunts, screams, squeaks, and whimpers.

^b"Nonsubmissive" calls include pant hoots and hoots, barks, food grunts and aaas, coughs, copulation screams, and hoos. See text for details.

Second, mean vocalization rates for all calls together, and for "submissive" and "nonsubmissive" calls, were computed for the three party types separately. By dividing social context into three categories based on subgroup composition, specific social contexts are isolated that may be responsible for potential differences in vocal behavior.

Third, results from the above party type analysis for "submissive" vs. "nonsubmissive" calling rates were compared with data from Marler and Tenaza [1977]. The number of occurrences of each call type recorded for an age/sex class divided by the number of individuals in that class were taken from Table 3 in Marler and Tenaza [1977] and converted to percentages for each class. In analogous fashion, vocalization rates for specific call types at Kibale were converted to percentages of the total call rate for each rank class in each type of party. Converted data from Marler and Tenaza [1977] were then compared to data from Kibale for each of the three different party types.

RESULTS

Vocalization Rates in All Parties Combined

Table IV shows mean total vocalization rates for the four rank classes (all parties combined). Individual rates from which these mean rates were computed are shown in Appendix A. Table IV also shows mean rates for "submissive" and "nonsubmissive" vocalizations.

Mean total vocalization rates did not differ significantly across rank classes ($F = .99, P > .1$), and "nonsubmissive" vocalization rates did not differ significantly between rank classes ($F = 2.67, P < .1$). However, submissive vocalization rates did differ significantly between rank classes ($F = 6.41, P < .005$). A posteriori analysis (Scheffe F-test) revealed the following between-group differences: adult females gave "submissive" vocalizations significantly more than high-ranking adult males ($F = 3.96, P < .05$), and subadult males gave "submissive" vocalizations significantly more than high-ranking adult males ($F = 3.42, P < .05$). All other a posteriori comparisons were nonsignificant.

Variation in Vocalization Rates Between Party Types for Each Rank Class

Table V shows mean total vocalization rates for the four rank classes in three different types of parties. Individual rates from which these mean rates were computed are shown in Appendices B and C. Because of small sample sizes, statistical tests were possible only for adult females in all parties, and for subadult

TABLE V. Comparison of Submissive and Nonsubmissive Call Rates for Three Different Party Types, and Observation Hours*

Rank class	Party type ^a	Mean calls per hour			Observation hours (N)
		Submissive ^b	Nonsubmissive ^b	Total	
AF	PT1	0.0 ± 0.0	0.3 ± 0.3	0.3 ± 0.3	24.3 (3)
	PT2	2.0 ± 1.8	0.7 ± 0.5	2.7 ± 2.3	11.9 (3)
	PT3	2.9 ± 1.8	2.0 ± 1.1	4.9 ± 2.0	32.0 (8)
SAM	PT1	—	—	—	—
	PT2	0.0 ± 0.0	0.1 ± 0.2	0.1 ± 0.2	9.3 (3)
	PT3	2.4 ± 1.0	1.9 ± 1.3	4.4 ± 2.2	50.3 (5)
AM2	PT1	—	—	—	—
	PT2	0.0	0.9	0.9	1.2 (1)
	PT3	0.4 ± 0.3	1.4 ± 0.9	1.8 ± 1.0	15.7 (4)
AM1	PT1	0.0 ± 0.0	8.7 ± 10.0 ^b	8.7 ± 10.0 ^c	3.7 (2)
	PT2	0.0	3.4	3.4	5.0 (1)
	PT3	0.0 ± 0.0	3.6 ± 2.3	3.6 ± 2.3	42.2 (4)

*Values represent means ± standard deviations; when only a single individual was sampled, only that individual's rate is given.—means there was no focal observation of that age/sex class in the party type. AF, adult female; SAM, subadult male; AM2, low-ranking adult male; AM1, high-ranking adult male; PT, party type; N, number of individuals on which the mean is based.

^aPT1, alone or with juveniles/offspring; PT2, with adult female(s) (± juveniles/offspring) only; PT3, with adult male(s) (if adult female or subadult male) or adult male(s) and adult female(s) (± juveniles/offspring) (if adult male).

^bFor classification of submissive and nonsubmissive calls, see footnote in Table IV.

^cThis exceptionally high value resulted from a high calling rate by SY for several days following his separation from ST [see Clark, 1991, for anecdotal description]. Although it is impossible to generalize from the rare occasions on which high-ranking adult males were observed alone, they nonetheless displayed vocal behaviors when alone that were never observed in other rank classes.

males (Party Type 2 vs. Party Type 3), and nonparametric tests were used (see Table V for the number of individuals in each sample group).

Adult females. Adult female total vocalization rates differed significantly between party types (Kruskal-Wallis, $H = 6.969$, $P < .05$). A posteriori analysis [Conover, 1980, p. 231] showed that adult females called significantly more in Party Type 3 than in Party Types 1 and 2 (no significant difference between Party Types 1 and 2).

Adult female "submissive" vocalization rates differed significantly between party types (Kruskal-Wallis, $H' = 6.025$, $P < .05$, where H' is corrected for ties). A posteriori analysis [Conover, 1980, p. 231] showed that adult females used "submissive" vocalizations significantly more in Party Type 3 than in Party Type 1 (other comparisons nonsignificant). Party type also significantly influenced "non-submissive" vocalization rates (Kruskal-Wallis, $H = 7.693$, $P < .05$). A posteriori analysis [Conover, 1980, p. 231] showed that adult females used "nonsubmissive" vocalizations significantly more in Party Type 3 than in Party Types 1 and 2 (no significant difference between Party Types 1 and 2).

Subadult males. Subadult males vocalized at significantly higher rates in Party Type 3 than in Party Type 2, for all calls, "submissive" calls, and "nonsubmissive" calls (Mann-Whitney, $U = 15$, $P < .05$ for all three).

Variation in Vocalization Rates Between Rank Classes for Each Party Type

Nonparametric statistical tests were also used to determine if individuals of different rank classes vocalized at different rates in the three types of parties in

which they were observed. Because of small sample sizes in some categories, statistical tests were possible only for Party Type 2 (adult females vs. subadult males) and Party Type 3 (comparing all rank classes) (see Table V for the number of individuals in each sample group).

Vocalization rates in Party Type 2 for adult females and subadult males did not differ significantly for all calls, "submissive" calls, or "nonsubmissive" calls (Mann-Whitney $U = 8, 8,$ and $7.5,$ respectively; $P > .1$ in all cases).

Vocalization rates in Party Type 3 did not differ significantly between the four rank classes for all calls (Kruskal-Wallis, $H' = 7.446, P < .1$) or "nonsubmissive" calls (Kruskal-Wallis, $H' = 4.166, P > .1$). A significant difference was found for "submissive" calls ($H' = 14.701, P < .05$). A posteriori analysis [Conover, 1980, p. 231] revealed that adult females and subadult males both gave "submissive" vocalizations significantly more than low- and high-ranking adult males ($P < .05$ in all cases). No other significant differences were found between groups.

Comparison With Marler and Tenaza [1977]

Figure 1 shows the proportion of all vocalizations given by individuals in each rank class that were "submissive" vs. "nonsubmissive" in each of the three party types analyzed from Kibale, compared with converted ad lib data from Marler and Tenaza [1977, Table 3]. In Marler and Tenaza, the proportion of submissive calls was relatively high for adult females, successively less for subadult males and then low-ranking adult males, and least for high-ranking adult males. Since hoos were included with whimpers in Marler's [19] catalog, the proportion of submissive calls should be slightly elevated for Marler and Tenaza in Figure 1.

The proportion of submissive calls in my study varied greatly between party types. In Party Type 1, neither adult females nor high-ranking adult males were observed to give a submissive vocalization. In Party Type 2, only adult females were observed to give submissive vocalizations. In Party Type 3, the proportion of submissive calls given by adult females and subadult males is nearly identical to that shown for the Marler and Tenaza [1977] study. Kibale low-ranking adult males had a somewhat lower proportion of submissive vocalizations than Marler and Tenaza's [1977], while Kibale high-ranking adult males were not observed to give any submissive vocalizations during focal observation.

Since sampling techniques in the two studies were so dissimilar, no statistical tests were applied.

DISCUSSION

The results of this study indicate that vocal production by Kibale chimpanzees is dependent on the rank of the vocalizer and the composition of subgroups in which individuals are observed. Total vocalization rates did not differ between rank classes in all parties combined (Table IV), a result similar to that reported by Marler [1976]. However, when vocal production was examined in relation to social context, a clear rank difference emerged (Table V). Females rarely vocalized when alone (Party Type 1), primarily gave submissive-type vocalizations when with adult females only (Party Type 2), and gave submissive and nonsubmissive vocalizations most when in larger, mixed parties (Party Type 3). Although not sampled as well, subadult males and low-ranking adult males demonstrated a pattern similar to adult females. Unlike lower ranking individuals, however, high-ranking adult males were observed to vocalize at relatively high rates in all party types. This made adult males appear more sociable than other classes of individuals,

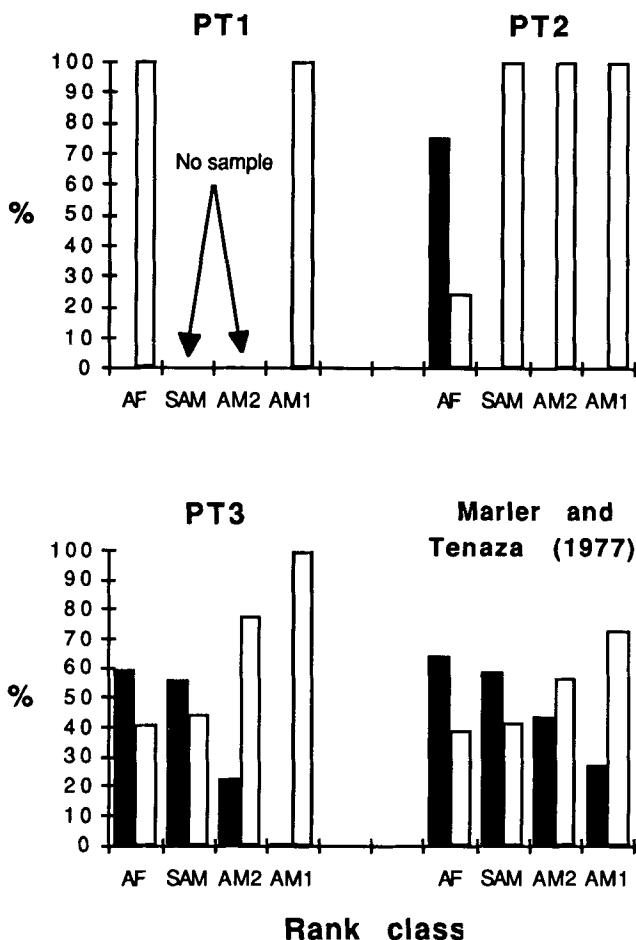


Fig. 1. Percentage of vocalizations which were "submissive" vs. "nonsubmissive": comparison of data for three party types (PT1-3) from Kibale study with Gombe data adapted from Marler and Tenaza [1977, Table 3]. Solid bars, "submissive" calls; open bars, "nonsubmissive" calls. See text for details.

consistent with the picture that emerged from a previous analysis of association and grooming data from Kibale [Clark, 1991; Wrangham et al., 1992].

Comparison of the proportion of submissive calls given in different party types with data from Marler and Tenaza [1977] emphasizes the importance of party type for understanding patterns of vocal behavior in wild chimpanzees (Fig. 1). The proportion of submissive vs. nonsubmissive calls was most nearly equal for all classes of Kibale chimpanzees in Party Type 3. This result resembled closely the pattern reported by Marler and Tenaza [1977: data modified from Table 3] for Gombe chimpanzees. Moreover, if hoos had been included with whimpers as submissive vocalizations in the Kibale sample (as they were in the Gombe study), the proportion of submissive calls would have been slightly higher and the match improved. The comparison suggests that although individuals of all rank classes may share in the production of all call types [Marler, 1976], the degree to which they do so is highly dependent on the composition of subgroups individuals find

themselves in. The virtual absence of grunting among adult males at Kibale is as yet unexplained, but may simply reflect a period of relative social stability in this population. It is apparently an obvious difference from at least Gombe chimpanzees (R.W. Wrangham, personal communication).

The similarity between the Kibale data for mixed parties and the Marler & Tenaza data (Fig. 1, bottom) suggests that exclusive observation at the Gombe provisioning area produced only a partial picture of sex differences in chimpanzee vocal behavior. Nonetheless, it is notable that the pattern of vocal behavior reported by Marler [1976] is consistent with that found among unprovisioned Kibale chimpanzees under some natural conditions. Kibale chimpanzees tended to form large, mixed parties at trees rich in fruit, and it was at these trees that the majority of my observations were made. The similarity between the Gombe data and those for Party Type 3 at Kibale therefore is in opposition to recent arguments that provisioning drastically alters the natural behavior of wild chimpanzees [for example, see Power, 1986]. Rather it appears that, at least from the point of view of quantitative patterns of vocal production, behavioral contexts associated with provisioning may closely approximate natural situations at large fruiting trees where food is concentrated in space and is superabundant, and where large, mixed associations of chimpanzees typically feed.

Social Relationships and Vocal Production

Differences in vocal production between higher and lower ranking chimpanzees may reflect differences between individuals in the costs and benefits of associating in parties, pointing to the importance of social relations in determining patterns of vocal behavior. I will consider the four rank classes in turn.

Although adult females are capable of producing all calls in the vocal repertoire, there are two reasons why it might benefit them to remain quiet under most circumstances. First, Hunt [1992] found that higher ranking male chimpanzees monopolized the best feeding sites. As the lowest ranking individuals in the community, females probably suffer the most from feeding competition in large parties. If food is the critical resource for females from the point of view of maximizing their individual fitness [Wrangham, 1979a], then they should be least able to afford this competition, and might therefore refrain from advertising their location with loud, interparty calls. Second, infant chimpanzees at other study sites are known to be targets of fatal aggression from both adult females and adult males in their own and neighboring communities [Goodall, 1977; Kawanaka, 1981; Norikoshi, 1982; Hamai et al., 1992]. Adult females themselves may also be the recipients of intra- and intercommunity male aggression [Goodall et al., 1979; Nishida et al., 1985; Goodall, 1986]. We might therefore again surmise that females with infants would be the least inclined to broadcast their location and attract potentially unfriendly conspecifics.

High-ranking adult males, on the other hand, tended to vocalize in all types of parties, and their vocal production was dominated by loud, nonsubmissive calls. There are at least three ways in which these males might benefit by broadcasting information about their identity and location. First, group size is advantageous in intergroup encounters in wild chimpanzees [Nishida et al., 1985], and calling may facilitate the aggregation of cooperative males [Wrangham, 1977]. Goodall [1986] observed that choruses of loud vocalizations from neighboring chimpanzees caused parties to move away from the source of the calls. Thus loud calls apparently also function directly to regulate intergroup spacing. Second, the importance of coalitions for establishing and maintaining dominance rank within chimpanzee communities is well established [Bygott, 1979; de Waal, 1982; Nishida, 1983]. Loud

calls may provide a means by which coalition partners can maintain contact with one another while foraging or traveling separately (Mitani, unpublished data). Finally, loud calling could attract potential mates [Wrangham, 1977].

Like adult females, subadult males were generally quiet when associating with females (they were rarely observed alone, but it is likely that they were quiet at these times as well), and more vocal when they were with adult males. Data on dominance interactions from Kibale [Clark, 1991; Wrangham et al., 1992], which for the most part were observed at food trees, indicated that subadult males were the class of individuals most likely to be targets of violent aggression from adult males. These aggressive interactions frequently interrupted or prevented subadult males from feeding. It is possible that the lack of loud calling by subadult males associating with females also reflects their need to minimize feeding competition (as well as the frequency of potentially dangerous physical interactions) during an important stage of their physical maturation.

It is puzzling why adult females and subadult males increased their nonsubmissive vocalization rates when they were with adult males. One explanation is that if it benefits adult males to advertise the size of their party, then so too might it benefit females and subadult males, *once* they are in the company of friendly adult males. Intercommunity encounters between groups of similar size can result in prolonged visual and vocal displays [Goodall, 1986], which presumably may escalate into violent physical confrontations. However, when it is evident from vocal choruses that a neighboring party contains more individuals than one's own, silent retreat generally ensues [Goodall, 1986]. As the most vulnerable targets of physical aggression, females and subadult males would benefit greatly by promoting the retreat of potential aggressors.

Finally, the vocal behavior of low-ranking adult males appeared intermediate between that of the highest and lowest ranking individuals in the community. Low-ranking adult males, like high-ranking ones, had low rates of submissive vocalizations in all types of parties, consistent with their position of relatively high rank compared to females and subadult males. Unlike high-ranking males, however, the rate of nonsubmissive call production among low-ranking adult males was also low in all party types. This seems peculiar since one might expect that they would derive the same benefits from loud calling as high-ranking adult males. Since feeding competition is probably less important for low-ranking adult males than for subadult males, an alternative cost is that loud calling is a prerogative of high-status males, and calling by potentially competitive low-ranking adult males constitutes a dominance challenge that carries the risk of physical confrontation.

CONCLUSIONS

1. Individuals were divided into four rank classes: adult female, subadult male, low-ranking adult male, and high-ranking adult male. Individual vocalization rates were calculated according to whether an individual was in one of three types of subgroup associations, or parties: alone or with dependent offspring; with one or more adult female(s) only (\pm infants, juveniles, and subadult females, but without adult or subadult males); with at least one adult male (for females and subadult males) or one adult female and one adult male (for adult males).

2. Although total vocalization rates were similar for all rank classes in all parties combined, different types of vocalizations were produced at different rates by the four rank classes depending on the type of party they were in. Broadly speaking, adult females and subadult males were quiet when alone, gave mostly "submissive" calls when with adult females, and gave "submissive" and "nonsub-

missive" calls most when with adult males; low-ranking adult males rarely gave "submissive" calls in any party, but also had relatively low rates of "nonsubmissive" calls throughout. High-ranking males rarely gave "submissive" calls, and had high rates of "nonsubmissive" calls in all party types.

3. Patterns of vocal behavior were interpreted in light of possible social strategies employed by different classes of individuals. Minimal vocal production by females and subadult males when they were alone or with adult females may reflect the need to avoid feeding competition and/or aggression by adult males; by giving loud calls when they are with adult males, females and subadult males may help to deter intergroup aggressive encounters. Unlike higher ranking individuals, low-ranking adult males had comparatively low "nonsubmissive" vocalization rates in all party types. It is suggested that certain loud calls are an expression of dominance status, such that their use by low-ranking individuals may constitute a dominance challenge. A number of benefits of loud calling are discussed for high-ranking adult males, including the attraction of allies and mates, and regulating intergroup spacing. Further research is needed to test these possibilities.

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APPENDIX A. Individual Vocalization Rates (Calls/Hr) in All Parties Combined, and Observation Hours

Vocalization	Adult females (AF)										Subadult males (SAM)						
	LP	CE	AR	AY	KY	TD	FG	YS	KL	Mean	YB	MS	AJ	RZ	NJ	Mean	
Pant hoot	0.374	0.330	0.000	0.000	0.000	0.000	0.063	1.111	0.000	0.235	0.267	0.688	0.066	0.779	0.299	0.420	
Hoot	0.037	0.000	0.327	0.000	0.000	0.190	0.190	0.000	0.043	0.075	0.214	0.115	0.066	0.097	0.000	0.098	
Bark	0.112	0.659	0.327	0.667	0.976	0.317	0.317	0.000	0.129	0.398	0.107	0.344	0.131	1.364	0.299	0.449	
Cough	0.112	0.000	0.000	0.000	0.000	0.063	0.063	0.000	0.000	0.022	0.000	0.000	0.000	0.000	0.100	0.020	
Hoo	0.411	1.978	0.490	3.333	0.488	0.000	0.000	0.278	0.043	0.878	0.320	0.229	0.131	1.169	0.199	0.410	
Food grunt	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.053	0.459	0.066	0.195	0.199	0.194	
Cop. scream	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.556	0.000	0.069	0.000	0.000	0.000	0.000	0.000	0.000	
Whimper	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.574	0.066	0.195	0.000	0.167	
Squeak	0.000	0.000	0.000	0.667	0.000	0.063	0.063	0.278	0.129	0.142	0.053	0.115	0.656	0.000	0.199	0.205	
Scream	0.037	0.000	0.000	0.000	0.000	0.127	0.127	0.000	0.086	0.031	0.107	0.688	0.393	0.292	0.299	0.356	
Grunt	0.486	2.637	3.433	0.667	1.463	1.270	1.270	3.611	0.472	1.755	0.641	1.033	0.590	2.532	1.395	1.238	
Nonsubmissive ^a	1.047	2.967	1.144	4.000	1.463	0.635	0.635	1.944	0.215	1.677	0.961	1.836	0.459	3.604	1.096	1.591	
Submissive ^a	0.523	2.637	3.433	1.333	1.463	1.460	1.460	3.889	0.687	1.928	0.801	2.409	1.705	3.019	1.894	1.966	
Total	1.570	5.604	4.578	5.333	2.927	2.095	5.833	3.605	1.762	4.245	2.164	6.623	2.990	3.557			
Observation hours	26.8	3.0	6.1	1.5	2.1	15.7	3.6	23.3	18.7	8.7	10.3						

Vocalization	Low-ranking adult males (AM2)					High-ranking adult males (AM1)				
	BB	LB	LM	SL	Mean	SY	ST	TU	BF	Mean
Pant hoot	0.000	0.349	0.732	0.000	0.270	2.472	0.353	2.466	0.560	1.463
Hoot	0.000	0.349	0.488	0.659	0.374	0.314	0.353	1.644	0.560	0.718
Bark	0.291	0.262	0.488	0.000	0.260	0.118	0.059	0.411	0.204	0.198
Cough	0.000	0.087	0.000	0.000	0.022	0.000	0.000	0.000	0.051	0.013
Hoo	0.874	0.611	0.732	0.000	0.554	0.628	1.472	2.055	0.611	1.191
Food grunt	0.000	0.262	0.000	0.000	0.066	0.471	0.177	0.411	0.051	0.277
Cop. scream	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Whimper	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Squeak	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Scream	0.000	0.175	0.000	0.000	0.044	0.000	0.000	0.000	0.000	0.000
Grunt	0.000	0.262	0.244	0.659	0.291	0.000	0.000	0.000	0.051	0.013
Nonsubmissive	1.165	1.921	2.439	0.659	1.546	4.003	2.414	6.986	2.037	3.860
Submissive	0.000	0.437	0.244	0.659	0.335	0.000	0.000	0.000	0.051	0.013
Total	1.165	2.358	2.683	1.319	1.881	4.003	2.414	6.986	2.088	3.873
Observation hours	3.4	11.5	4.1	1.5	25.5	17.0	2.4	19.6		

^aNonsubmissive subtotal includes pant hoot through copulation scream; submissive subtotal includes whimper through grunt.

APPENDIX B. Individual Vocalization Rates (Calls/Hr) for Those Individuals Observed in Party Types 1 and 2, and Observation Hours

Vocalization	Party type 1 (alone ± juveniles/infants)										Party type 2 (with adult female(s) ± juveniles/infants)									
	Adult females (AF)					High-ranking adult males					Adult females (AF)					Subadult males (SAM)				
	LP	FG	KL	Mean	SY	BF	Mean	Call	LP	AR	KL	Mean	YB	MS	AJ	Mean	LB	AM1 ^a		
Pant hoot	0.000	0.326	0.000	0.109	12.000	0.000	6.000	Ph	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.800		
Hoot	0.154	0.000	0.000	0.051	0.000	1.333	0.667	Ht	0.000	0.000	0.261	0.087	0.000	0.000	0.000	0.000	0.000	0.200		
Bark	0.000	0.000	0.000	0.000	0.000	0.000	0.000	Bk	0.000	0.316	0.261	0.192	0.000	0.000	0.000	0.000	0.857	0.000		
Cough	0.000	0.000	0.000	0.000	0.000	0.000	0.000	Co	0.202	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.000	0.000		
Hoo	0.462	0.000	0.068	0.176	1.846	0.000	0.923	Ho	0.000	0.947	0.000	0.316	0.000	0.000	0.000	0.000	0.000	1.400		
Food grunt	0.000	0.000	0.000	0.000	2.308	0.000	1.154	Fg	0.000	0.000	0.000	0.000	0.000	0.000	0.333	0.111	0.000	0.000		
Cop. scream	0.000	0.000	0.000	0.000	0.000	0.000	0.000	Cs	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
Whimper	0.000	0.000	0.000	0.000	0.000	0.000	0.000	Wh	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
Squeak	0.000	0.000	0.000	0.000	0.000	0.000	0.000	Sq	0.000	0.000	0.783	0.261	0.000	0.000	0.000	0.000	0.000	0.000		
Scream	0.000	0.000	0.000	0.000	0.000	0.000	0.000	Sc	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
Grunt	0.000	0.000	0.000	0.000	0.000	0.000	0.000	Gr	0.000	3.474	1.826	1.767	0.000	0.000	0.000	0.000	0.000	0.000		
Nonsubmissive ^b	0.615	0.326	0.068	0.336	16.154	1.333	8.744	Non	0.202	1.263	0.522	0.662	0.000	0.000	0.333	0.111	0.857	3.400		
Submissive	0.000	0.000	0.000	0.000	0.000	0.000	0.000	Sub	0.000	3.474	2.609	2.027	0.000	0.000	0.000	0.000	0.000	0.000		
Total	0.615	0.326	0.068	0.336	16.154	1.333	8.744	Total	0.202	4.737	3.130	2.690	0.000	0.000	0.333	0.111	0.857	3.400		
Observation hours	6.5	3.1	14.8		2.2	1.5		Hrs	4.9	3.2	3.8		3.3	3.0	3.0		1.2	5.0		

^aAM2, low-ranking adult male; AM1, high-ranking adult male.

^bNonsubmissive subtotal includes pant hoot through copulation scream; submissive subtotal includes whimper through grunt.

APPENDIX C. Individual Vocalization Rates (Calls/Hr) in Party Type 3 and Observation Hours*

Vocalization	Adult females (AF)										Subadult males (SAM)					
	LP	CE	AR	KY	TD	FG	YS	KL	Mean	YB	MS	AJ	RZ	NJ	Mean	
Pant hoot	0.904	0.330	0.000	0.000	0.000	0.000	1.111	0.000	0.293	0.387	1.108	0.082	0.792	0.314	0.536	
Hoot	0.000	0.000	1.319	0.000	0.000	0.471	0.000	0.000	0.224	0.309	0.185	0.082	0.099	0.000	0.135	
Bark	0.271	0.659	0.659	0.667	0.583	0.785	0.000	0.622	0.531	0.155	0.554	0.163	1.386	0.314	0.514	
Cough	0.181	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.105	0.021	
Hoo	0.633	1.978	0.000	0.333	0.583	0.000	0.278	0.000	0.851	0.464	0.369	0.163	1.188	0.209	0.479	
Food grunt	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.077	0.738	0.000	0.000	0.198	0.209	0.245	
Cop. scream	0.000	0.000	0.000	0.000	0.000	0.000	0.556	0.000	0.069	0.000	0.000	0.000	0.000	0.000	0.000	
Whimper	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.923	0.082	0.198	0.000	0.241	
Squeak	0.000	0.000	0.000	0.667	0.000	0.157	0.278	0.000	0.138	0.077	0.185	0.816	0.000	0.209	0.257	
Scream	0.090	0.000	0.000	0.000	0.000	0.314	0.000	0.622	0.128	0.155	1.108	0.490	0.297	0.314	0.473	
Grunt	1.175	2.637	6.593	0.667	1.748	3.141	3.611	1.244	2.602	0.928	1.662	0.735	2.574	1.463	1.472	
Nonsubmissive ^a	1.988	2.967	1.978	4.000	1.165	1.257	1.944	0.622	1.990	1.392	2.954	0.490	3.663	1.150	1.930	
Submissive ^a	1.265	2.637	6.593	1.333	1.748	3.613	3.889	1.865	2.868	1.160	3.877	2.122	3.069	1.986	2.443	
Total	3.253	5.604	8.571	5.333	2.913	4.869	5.833	2.487	4.858	2.552	6.831	2.612	6.733	3.136	4.373	
Observation hours	11.1	3.0	1.5	1.5	1.7	6.4	3.6	3.2	12.9	5.4	12.3	10.1	9.6			

Vocalization	Low-ranking adult males (AM2)					High-ranking adult males (AM1)				
	BB	LB	LM	SL	Mean	SY	ST	TU	BF	Mean
Pant hoot	0.000	0.422	0.763	0.000	0.296	1.550	0.446	2.466	0.236	1.174
Hoot	0.000	0.422	0.508	0.659	0.397	0.443	0.297	1.644	0.472	0.714
Bark	0.000	0.000	0.508	0.000	0.127	0.148	0.000	0.411	0.315	0.218
Cough	0.000	0.141	0.000	0.000	0.035	0.000	0.000	0.000	0.000	0.000
Hoo	0.645	0.703	0.763	0.000	0.528	0.369	1.485	2.055	0.944	1.213
Food grunt	0.000	0.000	0.000	0.000	0.000	0.517	0.223	0.411	0.000	0.288
Cop. scream	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Whimper	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Squeak	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Scream	0.000	0.281	0.000	0.000	0.070	0.000	0.000	0.000	0.000	0.000
Grunt	0.000	0.422	0.254	0.659	0.334	0.000	0.000	0.000	0.079	0.020
Nonsubmissive	0.645	1.686	2.542	0.659	1.383	3.026	2.450	6.986	1.966	3.607
Submissive	0.000	0.703	0.254	0.659	0.404	0.000	0.000	0.000	0.079	0.020
Total	0.645	2.389	2.797	1.319	1.787	3.026	2.450	6.986	2.045	3.627
Observation hours	3.1	7.1	3.9	1.5	13.6	13.5	2.4	12.7		

*Party type 3: individual adult female is with at least one adult male, with or without subadults, juveniles, and/or infants; individual subadult male is with at least one adult male, with or without adult females, subadults, juveniles, and/or infants; individual adult male is with at least one adult female and one adult male, with or without others.

^aNonsubmissive subtotal includes pant hoot through copulation scream; submissive subtotal includes whimper through grunt.