International Journal of Primatology, Vol. 17, No. 2, 1996

Effects of Contextual and Social Variables on Contact Call Production in Free-ranging Ringtailed Lemurs (*Lemur catta*)

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Received December 12, 1994; revised June 9, 1995; accepted August 25, 1995

*Ringtailed lemurs (*Lemur catta*) often emit a characteristic vocalization when resting as a troop. This "meow call" is believed to serve an intragroup contact function. I investigated the effects of behavioral context and proximity on call production and acoustic features of the vocalization in a free-ranging troop in the Berenty Reserve, Madagascar. When group members were dispersed, the meow call was given frequently, and the acoustic features of the call probably increased the locatability of the emitter. I evaluated social relationships among the troop members from grooming interactions and spacing data. I also studied the call exchange network among the troop members, the results of which indicate that calls are exchanged between the two subgroups of females, which they connect.*

KEY WORDS: ringtailed lemur; *Lemur catta*; contact call; call exchange; group cohesion; social relationship.

INTRODUCTION

In group-living primates, members of a troop need to communicate with each other in order to maintain cohesion. This communication may be based on physical contact, e.g., grooming, as well as on the transfer of visual or acoustic information. Contact calls occur in many species of primates. They maintain the cohesiveness of the group [prosimians (Macedonia, 1986), Old World monkeys (Gautier and Gautier, 1977; Gautier and Gautier-Hion,

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1988), New World monkeys (Snowdon, 1989), apes (Harcourt *et al.*, 1993)]. In addition, contact calls given by some species function in a rudimentary representational manner [vervet monkeys (Cheney and Seyfarth, 1982), spider monkeys (Masataka, 1986). Most contact calls share the properties of being tonal in structure and of relatively low frequency. Previous investigators noted that contact calls are often heard in rapid sequences involving two, or occasionally more, animals and that group members do not vocalize at random. A study on a squirrel monkey (*Saimiri sciureus*) contact call revealed that affiliated females were more likely to emit the calls consecutively than nonaffiliated animals were (Smith *et al.*, 1982). On the other hand, in Japanese macaques (*Macaca fuscata*), the distribution of contact calls is not related simply to affiliation. Mitani (1986) reported that the pattern of call exchange in a troop differed from that of affiliative interactions as measured by grooming. The two matriarchs of the kin groups frequently exchanged contact calls.

I observed a free-ranging troop of ringtailed lemurs (*Lemur catta*) at the Berenty Reserve, Madagascar, to investigate the effects of contextual and social variables on their emission of meow calls. The ringtailed lemur is diurnal and lives in groups averaging 12 to 24 individuals (Jolly, 1966). Vocalizations possessing the features of contact calls are often produced during daily activities ["meow call" of Jolly (1966)]. Variants of this call have been described by Andrew (1963) and Macedonia (1994) as moan and wail and by Petter and Charles-Dominique (1979) as cohesion miaouw. Macedonia (1986) recorded and spectrographically analyzed these vocalizations from eight semi-free-ranging individuals. Results of a discriminant function analysis indicated that statistical discrimination of individuals was possible on the basis of the acoustic differences in the calls. Thus, ringtailed lemurs possess the acoustic basis for individual recognition, but the way they employ the calls is still unknown.

METHODS

Study Site and Subjects

I conducted observations and recordings between August and December 1993 at the Berenty Reserve, southern Madagascar. Berenty is situated in an area of gallery forest surrounded by sisal plantations and the Mandrare River. The total area is approximately 200 ha (Jolly, 1972). I studied one troop of ringtailed lemurs (C2 troop). The troop contained seven adult males (≥3 years), six adult females, a subadult female (≥2 years), and three juveniles. This group has been identified and studied since 1989 (Koyama, 1991). Names of all the members are abbreviated to two letters of the alphabet. Sixteen animals in the C2 troop were the subjects of the focal animal sampling (Table I).

Data Collection

I sampled while the lemurs were most active, which is between 0600 and 1100 and between 1400 and 1800. Sampling was designed to provide equal observation times for each animal. I recorded all occurrences of vocalizations of a focal animal 2–4 m from the subject. In addition, I noted the focal animal's activity when calling and proximity to other group members within a radius of 3 m. I also scored activity and proximity (within a radius of 3 m) to other group members at 5 min intervals using a point sampling method (Altmann, 1974). I used a Sony NT-1 digital microrecorder and Sony ECM-672 and ECM-221 microphones to record vocalizations.

Data Analyses

Activities of focal animals are in one of three categories: resting, moving, or foraging. I compared calling frequency (number of calls emitted per minute) across the three contexts with a two-way analysis of variance

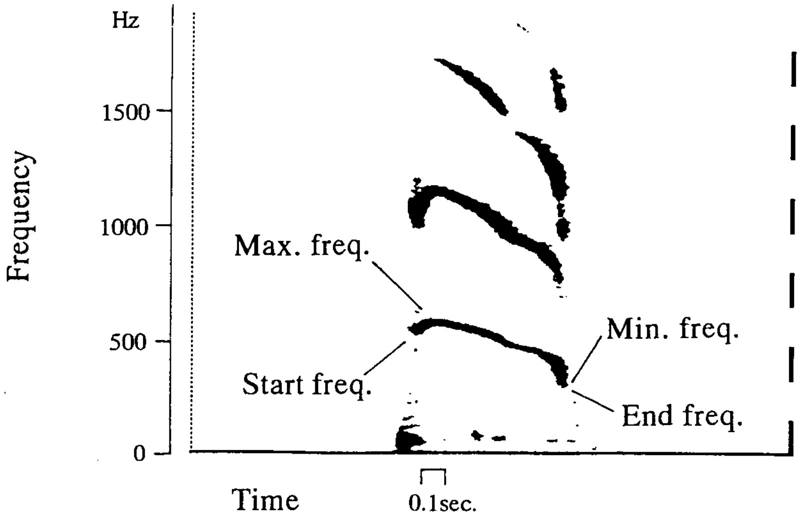

Fig. 1. Sound spectrogram of a meow call. Labels refer to the spectral measurements used in the analysis.

Table I. Individual Means and Standard Deviations by Variable[a]

Variable	OD (adult male)	RH (adult female)	SI (adult female)	MI (adult female)	KI (adult female)	OD90 (adult female)	ds (adult male)	nt (adult male)
Duration (sec)	0.651±0.166	0.501±0.198	0.390±0.112	0.410±0.208	0.448±0.141	0.630±0.214	0.394±0.172	0.535±0.252
Start freq. (Hz)	735±236	580±139	492±172	1143±496	580±150	644±277	836±294	1171±437
End freq. (Hz)	396±67	383±78	366±131	762±457	396±153	394±104	386±101	471±222
Max. freq. (Hz)	748±230	607±133	513±170	1192±494	622±146	685±277	875±278	1196±424
Min. freq. (Hz)	396±67	383±78	365±131	759±459	393±140	393±104	386±101	468±217
Peak position (%)	7.3±1.0	19.2±16.3	24.2±23.8	23.4±22.2	25.1±16.9	19.2±15.8	19.1±20.9	12.1±15.6
Max - min (Hz)	352±238	224±150	148±122	433±396	229±113	292±248	489±242	728±434
Max - start (Hz)	14±19	27±33	22±25	49±98	41±45	42±30	39±50	25±39
Median freq. (Hz)	572±121	495±79	440±139	976±434	507±131	539±169	631±170	832±258

Table I. Continued

Variable	da (adult male)	db (adult male)	nu (adult male)	mi90 (adult male)	MI91 (subadult female)	OD92 (juvenile female)	ki92 (juvenile male)	mi92 (juvenile male)
Duration (sec)	0.477±0.181	0.354±0.093	0.463±0.185	0.391±0.242	0.578±0.198	0.337±0.109	0.275±0.112	0.199±0.097
Start freq. (Hz)	815±442	1527±296	680±197	711±313	664±322	968±371	1403±400	1488±391
End freq. (Hz)	479±351	1187±332	422±170	666±369	659±386	726±344	1449±479	1419±478
Max. freq. (Hz)	845±437	1593±287	712±198	775±363	841±449	1020±379	1593±460	1548±400
Min. freq. (Hz)	479±350	1187±332	406±130	643±337	571±288	709±326	1347±436	1383±457
Peak position (%)	15.6±13.3	26.1±11.6	13.4±20.0	31.1±31.9	49.6±28.2	28.5±30.0	49.6±26.3	59.1±32.8
Max - min (Hz)	366±316	405±215	306±156	132±96	270±281	311±317	246±165	165±201
Max - start (Hz)	30±32	65±41	32±92	64±77	177±181	52±54	191±172	60±58
Median freq. (Hz)	662±363	1390±291	559±148	709±347	706±350	864±316	1470±440	1466±418

[a] Names of all the individuals are abbreviated to two letters of the alphabet.

(ANOVA) to determine the significance of the effects of context and individual on call production. I employed Sheffe's method for pairwise comparison (Sokal and Rohlf, 1981).

I numbered meow calls of high quality and chose 30 calls per individual ($N = 480$) at random via computer. I conducted acoustic analysis for those 480 calls with a Kay DSP Sonagraph 5500 using the narrow band filter, at a frequency range of 0–2.0 kHz. Measurements of acoustic features are restricted to the fundamental frequency (F_0). For each call I measured nine acoustic parameters: the duration, peak position (location of the maximum frequency relative to F_0 duration), start frequency, end frequency, minimum frequency, maximum frequency, frequency ranges (maximum minus minimum frequency, maximum minus start frequency), and median frequency [(maximum + minimum)/ 2] (Fig. 1). A summary of these measurements is in Table 1. I used a repeated-measures two-way ANOVA for the acoustic parameters to determine the significance of the effects of context and individuality on call structure (Sokal and Rohlf, 1981). It was not possible to analyze the effect of all three contexts in the ANOVA because the number of meow calls during foraging was too small. Moreover, one individual vocalized meow calls only while resting. The context factor had 2 levels—resting versus moving—and the individual factor had 15 levels.

I classified 30 calls of each lemur into two categories. In the first case, other individuals were present within a 3-m radius when the call was emitted, and in the second other animals were absent. I also numbered the point sampling data obtained at 5 min intervals and chose 30 samples per individual at random. I compared proximity to other group members when an individual vocalized with the point-sample data via a paired-comparisons t test. I used a repeated-measures two-way ANOVA to determine the significance of the effects of proximity and individual on call structure. The proximity factor had 2 levels and the individual factor had 15 levels because one individual vocalized meow calls only while others were absent. The data used in these parametric tests satisfy the assumption of normality.

I evaluated social relationships among troop members from grooming interactions and spacing data. I divided each grooming session into sampling periods of one minute duration. I did not consider the direction of grooming because most dyadic grooming is mutual in ringtailed lemurs. I analyzed spacing structure via a proximity index, as calculated from the formula

$$(P_{ab} + P_{ba}) \ / \ (U_a + U_b)$$

in which P_{ab} is the number of the point samples that individual B was seen within a 3-m radius of A when A was the focal animal, P_{ba} is the number of the point samples that A was seen within a 3-m radius of B when B was the focal animal, U_a is the total number of the point sampling units of A, and U_b is the total number of point samples for B. Applying hierarchical cluster analysis to this index allows proximity relationships within the troop to be visualized (Morgan *et al.*, 1976).

I analyzed call exchange data by noting emitter and responder. An individual emitting a call <4 sec before the focal animal's call, if any, is an emitter. An individual emitting a call <4 sec after the focal animal's call, if any, is a responder. Call exchange is one exchange of call emissions between two individuals. I exclude cases in which a third lemur vocalized <4 sec before the emitter's call.

RESULTS

Context of Vocal Emission

The frequency of meow calls recorded in each context is 0.29 ± 0.08/min while resting, 0.36 ± 0.28/ min while moving, and 0.04 ± 0.05/ min while foraging. The results of a two-way ANOVA reveal that the effect of the context factor is significant ($F = 14.05$, df = 2, $P < 0.001$), while that of the individual factor is not significant ($F = 0.70$, df = 15, ns). Pairwise comparison indicates that ringtailed lemurs emit meow calls more frequently while resting and moving than while foraging and that the frequency is not significantly different between resting and moving (resting vs. foraging, $t = 3.84$, df = 30, $P < 0.01$; moving vs. foraging, $t = 5.08$, df = 30, $P < 0.001$; resting vs. moving, $t = 1.24$, df = 30, ns).

Next, I examined the effects of context and individual on the acoustic parameters. Start frequency, end frequency, maximum frequency, and minimum frequency are highly correlated with median frequency (correlation coefficients were 0.93–0.96). Therefore, these four parameters are excluded, and I performed a two-way ANOVA on the remaining five (Table II). The results indicate that the effect of context is not significant for any parameter, while the effect of individual is significant for all parameters. The interaction term was significant for three parameters.

Effect of Proximity

Significantly more calls occurred when other animals were absent ($n = 15.9 \pm 5.5$) than when others were present ($n = 4.9 \pm 3.5$; $t = 5.88$, df = 15, $P < 0.01$), despite the fact that subjects had neighbors ≤3 m sig-

Table II. Results of Repeated-Measures Two-Way ANOVA Performed on Five Acoustic Parameters in Terms of the Context and Individuality

	Factor		
Variable	Context F (df = 1,418)	Individual F (df = 14,418)	Interaction F (df = 14,418)
Duration	0.12	13.92**	2.14*
Peak position	1.76	12.99**	2.51*
Max. - min. freq.	5.34	10.02**	1.12
Max. - start freq.	0.15	11.23**	0.76
Median freq.	0.66	39.32**	2.38*

*$P < 0.01$, two-tailed.
**$P < 0.001$, two-tailed.

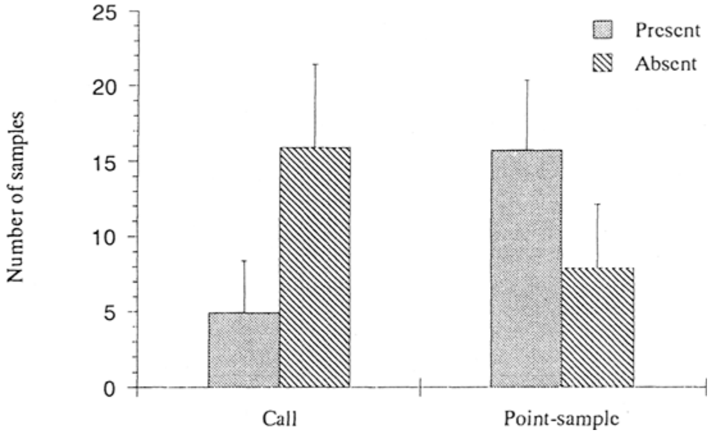

Fig. 2. Proximity of others to a focal animal emitting a meow call. Averages of 16 individuals are represented. T-bar indicates SD.

nificantly more often than not (number of samples: others present, 15.7 ± 4.6, others absent, 7.9 ± 4.2; $t = 8.18$, df = 15, $P < 0.01$; Fig. 2). Proximity while resting and foraging is not significantly different from that expected by chance ($\chi^2 = 3.24$, df = 1).

A two-way ANOVA, testing the effects of proximity and individuality on the acoustic parameters (Table III), revealed that the effect of the individual factor is significant for all parameters. The effect of proximity is significant for duration, maximum minus minimum frequency, and median frequency. For meow calls emitted when there were no other animals within a 3-m radius, duration was shorter, maximum minus minimum frequency was greater, and median frequency was higher than those recorded when others were present.

Table III. Results of Repeated-Measures Two-Way ANOVA Performed on Five Acoustic Parameters in Terms of the Proximity and Indivudality[a]

	Factor			
Variable	Proximity F (df=1,308)	Individual F (df=14,308)	Interaction F (df=14,308)	Proximity
Duration	11.59**	8.62**	1.52	Present (0.53±0.20 sec) >Absent (0.44±0.21 sec)
Peak positon	5.59	9.35**	1.57	
Max. - min. freq.	25.10**	6.70**	1.72	Present (194.2±194.6 Hz) <Absent (371.9±318.6 Hz)
Max. - start freq.	0.63	7.34**	2.36*	
Median freq.	15.06**	17.72**	1.15	Present (593.7±367.7 Hz) <Absent (750.2±357.5 Hz)

[a] Numerical values are show in in the final column for the three acoustic parameters on which effects of proximity were significant.

*$P < 0.01$, two-tailed.

**$P < 0.001$, two-tailed.

Social Relationships and Call Exchange Network

The results of hierarchical cluster analysis are shown in Fig. 3. I excluded three juveniles from the following analysis to simplify the expression of social relationships. Females formed the core of the troop, as can be seen from the two large central clusters, while males were peripheral. One cluster includes an adult female OD and her daughter OD90; the other consists of an adult female MI and her daughter MI91. Males were likely to be alone, though nt and nu formed a cluster distant from females. The same tendency was apparent in grooming interactions (Fig. 4). The average length of a grooming session is 6.8 min (SD, 12.0 min). For females, pairs for which grooming sessions exceeded the average + SD could be roughly divided into two groups. One included MI, MI90, and RH; the other, OD, OD90, SI, and KI. This is consistent with the results of the spacing structure analysis. Grooming interactions for males occurred less frequently than those among females did.

I recorded 89 call exchanges for 50 dyads. Seventy-one exchanges were of sufficient quality to measure the inter-call interval. The average intercall interval is 0.65 sec (SD, 0.71 sec) and the range is between -0.18 and 2.91 sec. Twenty exchanges were between males and 53 between females. Numbers of exchanges between same-sexed individuals occurred significantly more often than expected by chance ($\chi^2 = 30.3$, df = 1, $P < 0.01$). Moreover, there were significantly more same-sexed dyads for which at least one exchange was observed (11 male–male; 27 female–female, $\chi^2 = 10.7$, df = 1, $P < 0.01$). The average number of exchanges is 1.14 occurrences per

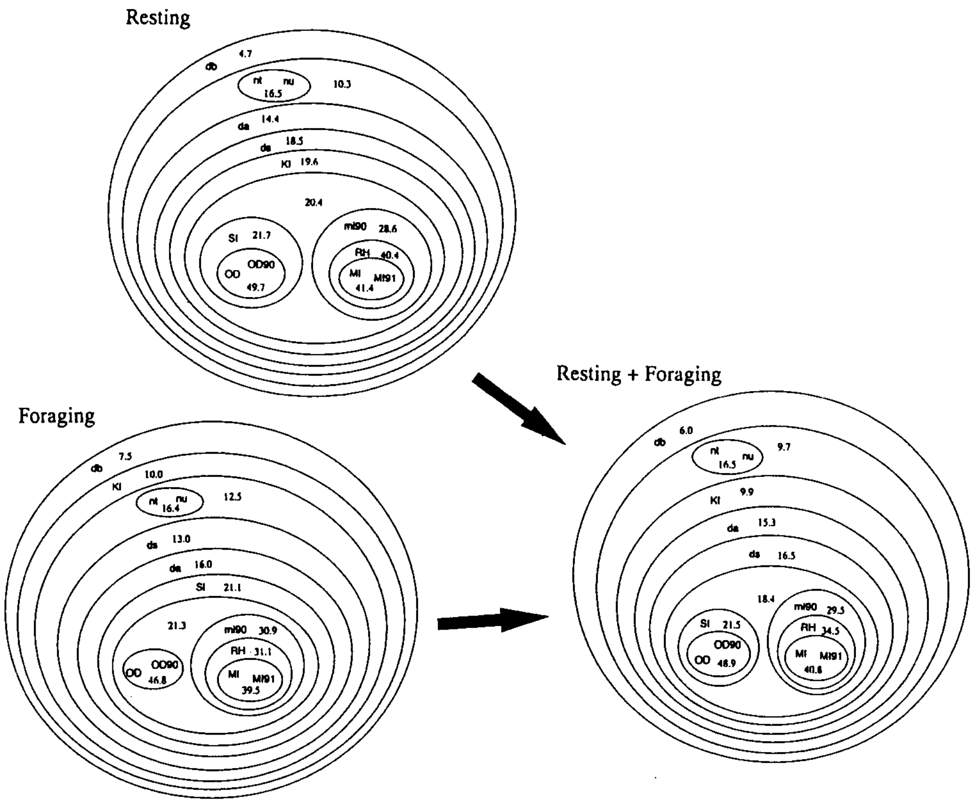

Fig. 3. Spacing structure of the troop during resting and foraging, obtained by hierarchical cluster analysis of individuals within a 3-m radius of the focal animal. Capital letters indicate females and lower case letters indicate males. The value connected to each circle indicates the proximity index explained under Methods.

dyad (SD, 1.80). The sociogram of call exchange in the troop is in Fig. 5. The pattern of call exchange differed from that of grooming interactions, and I observed exchanges between the two subgroups of females illustrated in Fig. 3.

DISCUSSION

The ringtailed lemurs called more frequently while resting and moving than while foraging, although there was no significant difference in proximity between resting and foraging. In some group-living primates, there is intra-group feeding competition (Janson and van Schaik, 1988). Indeed, Sauther (1993) reported that in free-ranging ringtailed lemur troops, 86% of agonistic interactions occurred over access to food resources. It may be disadvantageous for a lemur to call and to draw the attention of other members in a foraging situation. Moreover, the cluster analysis illustrates the difference of spacing structure between these two activities. The tendency to form sub-

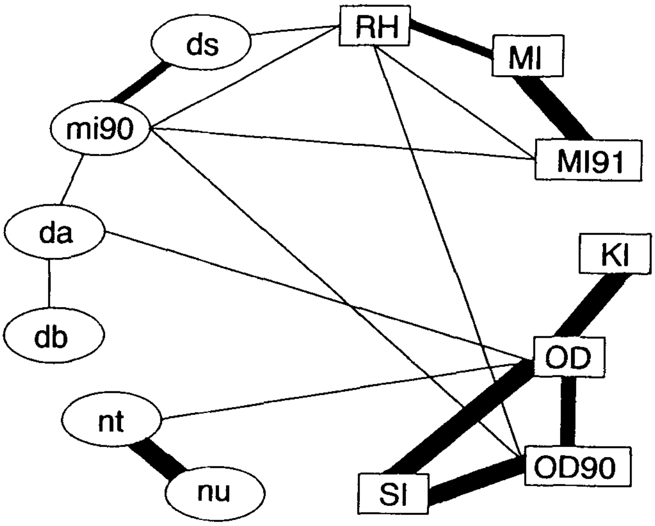

Fig. 4. Sociogram of grooming interaction among the troop members. Only frequency indices greater than the mean ($\bar{X}$) are shown by lines. Scale: thin line = $\bar{X}$ - $\bar{X}$ + SD; medium-width line = $\bar{X}$ + SD - $\bar{X}$ + 2 SD; thick line ≥ $\bar{X}$ +2 SD. Circles indicate males and squares indicate females.

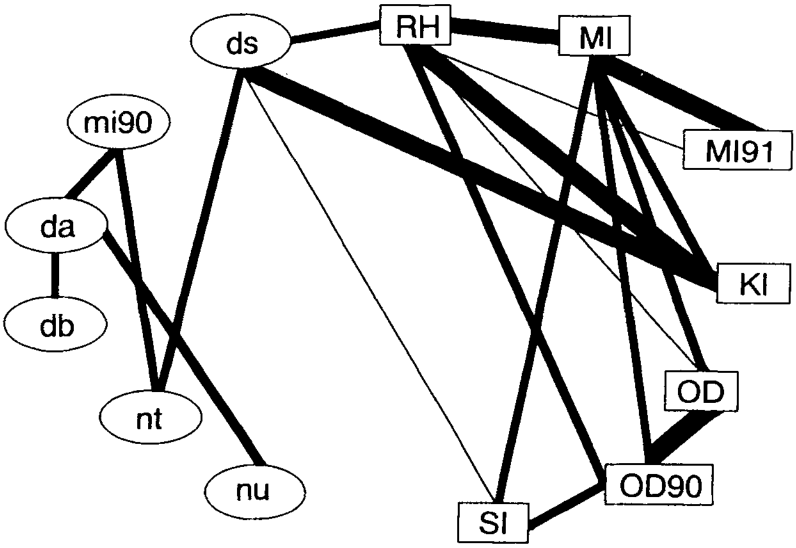

Fig 5. Exchange network of the meow call among the troop members. Procedure of analysis as in the legend to Fig. 4.

groups was higher during resting than foraging, which would seem to influence the calling behavior.

Ringtailed lemurs emit meow calls frequently when other group members are not nearby. Considering that the ringtailed lemur is a gregarious primate, it is not surprising that in the point sampling data; other animals were within a 3-m radius of the subject significantly more often than not. Absence of nearby conspecifics often, though not always, indicates that the troop members are dispersed. The above results provide support for the hypothesis that meow calls function to maintain group cohesiveness, which is also suggested by acoustic features of the calls. The results of the ANOVA indicate that proximity rather than context influenced the acoustic parameters. When other group members were distant, ringtailed lemurs emitted calls of shorter duration, higher pitch, and stronger frequency modulation than when others were nearby. Frequency modulation is an important feature of acoustic communication in nonhuman primates (e.g., Masataka, 1983; Newman *et al.,* 1983). Sounds that are strongly modulated in frequency are much easier to localize than sounds with little frequency modulation are. For example, Snowdon and Hodun (1981) reported that pygmy marmosets (*Cebuella pygmaea*) maximize locatability when caller and recipient are far apart in the forest by using strongly frequency-modulated calls. Brown *et al.* (1978) found that Japanese macaques can localize the source of stimulus sounds more easily when frequency-modulated calls are played back than when nonmodulated sounds are broadcast. High-pitched sounds also seem salient to macaques. Japanese macaques frequently exchange contact calls (Sugiura, 1993). Tanaka *et al.* (1993) conducted a playback experiment in which two types of contact call stimuli—relatively high-pitched and low-pitched—were used. The response latency was shorter, and the number of responses was greater, to high-pitched calls than to low-pitched ones. Although no experiments have been conducted on sound localization in lemurs, these results concerning temporal cues can be applied to meow calls of ringtailed lemurs. High-pitched calls may draw the attention of others and frequency-modulated sounds may provide an important auditory cue for the location of group members.

The results of the ANOVA indicated strong effects of individual factors on all five acoustic parameters, which support the results of Macedonia (1986) on a semi-free-ranging troop. However, acoustic parameters were influenced by proximity, which reveals that meow calls have intraindividual variation as well as interindividual variation.

The pattern of interaction in call exchange is different from that in grooming, though the number of dyads that interacted more often than average in grooming is very similar to that in call exchange. Ringtailed lemurs have a multimale multifemale society that is female-bonded. Mitani (1986) studied the influence of intragroup relationships on call exchange in a troop of Japanese macaques that share these two traits with ringtailed lemurs. Matriarchs of the kin groups frequently exchanged calls with each other. Males seldom participated in the call exchange. Although kinship among the ringtailed lemurs of C2 troop that >3 years old is unknown, it is possible that the two subgroups of females were matrilineal kin groups. Close matrilineal kin prefer to groom one another and to remain in proximity more than nonkin in semi-free-ranging ringtailed lemurs (Taylor and Sussman, 1985). Ringtailed lemurs sometimes divide into several subgroups during their routine daily activities (Jolly, 1966; personal observation), and they appear to use meow calls to communicate with other subgroups. I observed call exchanges between the two subgroups of females, as well as within each of them, which seemed to connect the subgroups. Males nt and nu frequently interacted with each other in grooming, though I noted no exchange of meow calls between them. Unlike Japanese macaques, ringtailed lemur males often exchanged vocalizations. It is interesting to note that among males, only ds exchanged calls frequently with females. He was dominant over all other males in C2 troop.

Social communication among group-living primates involves nonphysical contact as well as physical contact (Marler, 1965). Acoustic contact and physical contact complement each other to maintain group cohesion. My results support the hypothesis that separated individuals in a group share a spatial map of group dispersion that may be based on acoustic information (Masataka and Symmes, 1986).

ACKNOWLEDGMENTS

I thank Prof. N. Koyama and Prof. K. Aoki for their guidance during the course of the study. I am also grateful to Prof. A. Jolly, Prof. M. Hiraiwa-Hasegawa, Dr. H. Crowley, Dr. C. Saito, Ms. L. Rakototiana, and many other people in Berenty for their help and encouragement, to the government of Madagascar Republic, and Mr. J. de Heaulme for allowing me to carry out field research at the Berenty Reserve, and to Mr. A. Randrianjafy, the director of Timbazaza Zoo, and Dr. T. Shima for their help in Madagascar. Acknowledgments are also due to Prof. N. Masataka, Dr. D. Hill, Dr. H. Sugiura, Dr. J. M. Macedonia, and one anonymous reviewer for their helpful comments on the manuscript. This study was supported by Grant 05041088 from the Ministry of Education, Science and Culture of Japan.

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