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The Song of the Indris (*Indri indri;* Primates: Lemuroidea): Natural History, Form, and Function

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The song of the largest Malagasy lemur was extensively studied in the field between 1972 and 1984. The song's structure is described, and the role of song in the natural history of Indri *is examined by relating the naturally occurring variability of different song parameters to the behavior of habituated groups and the composition of other groups in the population. The function of an* Indri *group's song is complex, varying according to the location and identity of animals hearing it. Territorial aspects of the song are considered in detail and the nature of primate territorial vocalizations is critically discussed.*

KEY WORDS: *Indri indri*; loud calls; song; territorial behavior.

INTRODUCTION

The development of research on primate loud calls, while appropriately concentrating on functional explanations and adaptations, has been limited to the anthropoid suborder. Indeed, a recent review of this topic omitted any reference to prosimian vocalizations (Byrne, 1982). Prosimians may, however, be especially suitable for studies of this kind because of a number of characteristics which limit variation in their behavioral responses: the discrete nature of their vocalizations (Marler, 1965), the comparatively small number of different calls, and the importance of another channel of com-

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munication (olfaction) in their social behavior. According to general ecological rules, primates emitting the loudest and most regular calls should be forest-living, territorial species living in small family groups (Clutton-Brock and Harvey, 1976). This paper discusses the role played by loud calls in the natural history of the lemur *Indri indri* in the eastern rain forests of Madagascar (Fig. 1), a species possessing just such a set of characteristics.

Forests inhabited by *Indri* resound each day to loud modulating calls emitted by two to four members of each group either spontaneously or in response to other groups' calls. The calls also infrequently follow strange noises, thunder, the calls of other species, or the presence of airplanes or large birds. The song of an *Indri* group, which consists of a discrete succession of these loud calls, lasts for between 40 sec and 4 min, occurs usually during the morning, is emitted at least once on most days, and can be detected by the human ear up to 2 km from its source under optimal conditions.

Indri possess a large membranous laryngeal sac presumably used in song production but there are no reported distinctive specializations of the hyoid bone or other laryngeal structures (Hill, 1953).

Loud calls which stimulate other groups of the same species to call are rare in primates. To date the presence of such "contagious" loud calls as a frequent mode of communication has been reported only for *Alouatta palliata* (Chivers, 1969), *Colobus guereza* (Ullrich, 1961), and monogamous species such as *Callicebus moloch* (Robinson, 1979, 1981, 1983), *Callicebus torquatus* (Kinzey *et al.*, 1977; Kinzey, 1981), *Hylobates lar* (Raemakers and Raemakers, 1984), *Hylobates muelleri* (Mitani, 1985), *Hylobates* spp. (Marshall and Marshall, 1976), and *Hylobates syndactylus* (Chivers, 1974). In *Alouatta, Callicebus moloch,* and *Hylobates* spp., males call on their own early in the morning, and except for *Aloutta,* both sexes call in the course of territorial border encounters later in the day (*loc. cit.*). For *H. syndactylus* and *Callicebus torquatus,* however, a different pattern exists: both sexes call together from a central part of their ranging area later in the day, and intergroup encounters are very rare [siamang (Chivers, 1974)] or nonexistent [titis (Kinzey and Robinson, 1983)]. This pattern of calling is most similar to that of *Indri.*

This paper describes the physical structure of *Indri* song and the patterns with which songs are emitted by habituated study groups and the groups surrounding them in the population. Functional aspects of the song are examined by discussion of the type and frequency of songs and the behavior accompanying them in a variety of social contexts. This information is used in a heuristic fashion to attempt to create an integrated model of the way the song functions for *Indri.*

Fig. 1. *Indri indri.* Adult female at Analamazoatra (Group V).

METHODS

The feeding and ranging ecology and some aspects of the behavior of *Indri* have been previously presented (Pollock, 1975a, 1977, 1979a,b). The singing behavior of *Indri* was studied for 15 months during 1972 and 1973 and for a further 3 weeks in 1978 in areas relatively well populated by *Indri* (the forest of Analamazoatra, 18°56′S 48°24′E; Vohidrazana, 10 km to the east; and Fierenana, 60 km to the north) in eastern Madagascar. Additional data were collected in the course of a 7-week visit to a number of forests in eastern Madagascar in 1984. Approximately 3000 hr were spent in the collection of behavioral data and singing information in the three study areas. During this time, data were obtained from 2943 songs, 45 of which were recorded on tape. The three main study groups were closely observed for a total period of 23 days every 6 weeks in the course of all-day group follows. Eight such 6-week sessions or "circuits" made up the year's field observations.

For each song in the sample, data were recorded on time of day, song duration, song distance (see below), a variety of song characteristics, number of individuals singing, song direction (see below), and duration of overlapping songs. The climatic conditions prevailing at the time of each call were monitored by recording rain, wind, and cloud cover on five-point subjective scales.

Song direction was recorded by aligning a prismatic compass needle with a vertical tree trunk estimated to be directly in line with the song's origin. Distance was estimated by combining cues of loudness and frequency attenuation together with the experience obtained by finding specific groups after they had sung. Throughout the study period *Indri* groups were found and observed by pacing in a straight line through the forest in the compass direction afforded by the above method. *Indri* groups were always located within a small margin of error in direction and within errors of distance of less than 20%. Categories of distance, where used, were formed to minimize the importance of mistakes in distance perception. *Indri* groups were always found within 200 m and usually within 100 m of their estimated position when judged to be 1000 m or less from the observer. Long-term behavioral observations of habituated study groups proved that *Indri* do not normally move or otherwise behave unusually before or after their singing bouts.

Singing behavior itself and details of participation by different group members in the song were elucidated by observation of three habituated *Indri* groups while they were singing. The composition of these main study groups is shown in Table I. All *Indri* groups observed in this study (n = 19) appeared to be composed of a single breeding adult pair and from one to three other, usually smaller individuals. The most reasonable explanation for these group composition observations is that *Indri* commonly live in

Table I. Composition of the Main *Indri* Study Groups, P, V, and IV

Group	Adult ♀	Adult ♂	Adult sized (03)	Subadult (02)	Juvenile	Infant	Total
P	1	1	1 (♂)	1 (♂)	1 (♀)	–	5
V	1	1				1 (♂)	3
IV	1	1	1 (♀)	1 (♂)		1 (♂)	5

nuclear family units with no generation overlap; but other forms of association may also occur (personal observation), and it is unclear how long the breeding adults of a group remain together. At least one breeding pair ranged together for at least 6 years in the same area; in two other cases animals changed ranging areas, mates or both between 1973 and the next observation in 1978.

Songs in the wild were recorded on a Nagra IVL portable tape recorder through a Sennheiser MD421N super-cardioid microphone on BASF standard and low-noise magnetic tape. Frequency response characteristics of all components were essentially linear over the range of frequencies from 50 Hz to 8 kHz. Recordings were made of the study groups' songs on 1 or 2 days at approximately 6-week intervals. The microphone was situated between 6 and 30 m from the calling animals, which were often quite dispersed and rarely faced the microphone. The song could be heard by the observer between 1000 and 2000 m from the source, depending on the topographical positions of the calling group and the observer, the wind's speed and direction, and the amount of intervening vegetation.

RESULTS

Introduction

Each song is often, but not always, introduced by a communal "roar" [*aboiements* (Petter, 1962)], which normally lasts between 1 and 5 sec, occupying a wide band of frequencies between 500 and 4000 Hz (Fig. 2). This call, which is identical to the aerial predator alarm call, precedes song in 87% of all calls. Although accurate quantification was not feasible, most roars are started by the adult male, the rest of the group joining in almost immediately. A pause of 0.5 to 2 sec separates the end of the roar from the song proper. The song can be defined as a vocal display in which one or more individuals emit a sequence of calls for 40–250 sec, each howl separated by short pauses. Having roared, individuals within the group participated

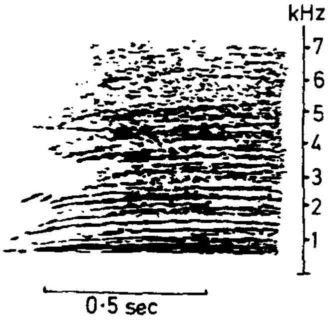


Fig. 2. Sonogram of a typical part of an *Indri* "roar"—the call which frequently introduces the song proper. The complete roar lasts between 1 and 5 sec.

differently in the course of the subsequent pattern of calls (see below). Occasionally, in study Group P, the adult male or the largest of the nonbreeding group members (03) would move during the roar, but usually animals either remained in their feeding positions or took up secure positions in a more central, lower part of the tree they already occupied. The calls were emitted in no particular direction (animals never turned to face the origin of preceding songs from other groups, for example), but the muzzle was pointed between 30 and 45° above the horizontal (Fig. 3). Petter and Peyrieras (1974) reported that *Indri* sing from the tops of trees at the highest parts of the ridge in order to achieve the greatest sound transmission distance. However, I did not observe such a pattern, and it is by no means certain that loud calls from such positions would necessarily carry the farthest because of refraction within the forest (Marten *et al.*, 1977; Waser and Waser, 1977). *Indri* sing from where they happen to be at the time and were never seen to climb higher before or during a song.

The song of *Indri* is seemingly a relaxed event despite the enormous power of the sound. On several occasions feeding continued between howls during the course of the song. Nonparticipants in a group's song were seen to groom, play, and feed while others sang.

Once the song ended, normal feeding and ranging activities were resumed, with no other overt change in behavior.

The Structure of *Indri* Song

Physical Analysis

Three *Indri* songs were structurally examined by means of a Kay sonograph and a real-time sound-spectrum analyzer (the Ubiquitous, Fig. 4). The song consists of a series of calls, each lasting from 1 to 4 sec, whose

Fig. 3. *Indri* singing at Vohidrazana (Group IV).

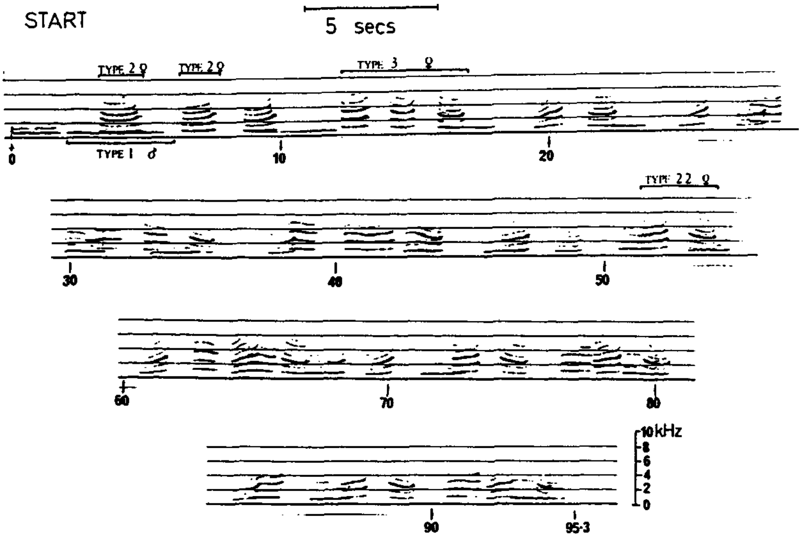


Fig. 4. Continuous sound spectrogram of a complete *Indri* song given by two adults (Group V). The song consists of three types of call and lasts for 95.3 sec.

main energy lies from 500 to 6000 Hz, separated by short pauses of up to 3 sec. Pure tones of the call appear with up to four harmonics and may be modulated by as much as 2000 Hz within each call. Some calls, however, remain essentially stationary in pitch.

During the course of the study different types of calls were recognized within each song. Some of this variation could be attributed to sexual dimorphism in the adults' song. In order of their first occurrence during the song, the different calls were separated into the following three types.

Type 1 Calls. Type I calls were long, low calls emitted only by adult males (Fig. 4). They had a fundamental frequency of 750 Hz, with an additional band at 1250 Hz, and subsequent harmonics. They were usually the first calls emitted by the adult and were most noticeable when only two animals were singing. Type I calls were up to twice as long (maximum observed duration, 5.2 sec) as other calls. Little frequency modulation occurred during the course of Type 1 calls.

Type 2 Calls. Type 2 calls were amplitude modulated, always ending in a pitch higher (by up to 2000 Hz) than that at which they began. These calls varied in their initial pitch but most of the energy of the calls resided between 700 and 3000 Hz. Described by Petter (1962) in his comparative report on lemur ecology, the calls last from 1.2 to 2.0 sec and may precede "mirror-image" calls which start at the termination frequency and end at the initial frequency of their predecessors (Fig. 4). Such paired calls (Type 2.2) were emitted by all singing individuals.

Type 3 Calls. Type 3 calls consisted of a series of three (occasionally four) successive calls, each starting lower in frequency than its predecessor and containing two slight frequency modulations (Fig. 4). They lasted for the same duration as Type 2 calls, which they very often followed in the song. All animals emitted these calls, but adult females developed the Type 3 pattern within the song earlier than other individuals. The first call of a Type 3 sequence was the loudest and highest (up to 9000 Hz) and contained the most energy in bands up to 6000 Hz.

In the three songs analyzed spectrographically, the actual percentage of time spent vocalizing by the adult females during the course of the whole song was 28.5 and 34.3% (Group P) and 43.8% (Group V), the remainder being gaps and pauses between calls and groups of calls. In two songs examined in detail, the expected amount of time that each pair would have called simultaneously (had they been calling independently of each other during the song) was calculated to be 10.1 sec (Group P) and 18.1 sec (Group V). These figures did not differ substantially from the observed duration of call overlap: 10.8 sec for Group P and 14.5 sec for Group V. In the course of the group's song, therefore, calls emitted by different individuals were not timed so as to achieve a greater overall production of sound.

In both groups the duration of the male calls exceeded that of the female calls. In Group P the male's call had a mean duration of 1.77 sec ($N = 17$), while those of the female averaged 1.36 sec ($N = 16$; $t = 4.26$; $P < 0.001$). In Group V the male's calls lasted for a mean time of 1.72 sec ($N = 12$), and the female's for 1.26 sec ($N = 20$; $t = 13$; $P < 0.001$). The call length of the two males in each group did not differ ($t = 0.734$; $0.4 < P < 0.5$) but those of the Group P female were significantly longer than those of the female in Group V ($t = 3.386$; $0.001 < P < 0.01$).

The difference in the proportion of time spent actually singing by Groups P and V females during the course of their group's song prompted a further examination of a sample of songs from tape recordings of the main study groups and their neighbors. Call rates were analyzed in a sample of 14 songs from at least eight different groups. The results (Table II) suggest that the total call rate is independent of the number of individuals singing and therefore of the group composition. Individuals in groups with fewer singers therefore call, on average, more frequently than those in larger singing groups. Further analysis of one song each from Groups P and V shows that this difference between groups, for the main study groups at least, is accounted for by the female's singing behavior only (Table III).

Individual Participation in the Song of an Indri *Group*

Individuals did not participate equally in a group's song, as supposed by Petter and Peyrieras (1974). For example, toward the end of the study,

Table II. *Indri* Song: Variation in the Rate of Calls Within Songs

Group	Date	Song duration (sec)	Number of (calls/sec)	Call rate
P	18.10.72	235	3 or 4	0.45
	27.11.72	143	3 or 4	0.57
V	26.10.72	95	2	0.57
	14.04.73	51	2	0.55
	16.12.72	65	2	0.65
	06.12.72	78	2	0.64
4	26.05.73	82	3 or 4	0.67
	26.05.73	67	3 or 4	0.58
5	21.04.73	32	2	0.53
	23.04.73	70	2	0.51
?	23.04.73	81	3	0.67
?	06.12.72	186	3	0.55
?	06.12.72	60	2	0.63
?	26.05.73	106	2	0.6
		Mean call rate (calls/sec)		
2-voice groups (N = 3)			3- or 4-voice groups (N = 3)	
0.59 (N = 8)			0.59 (N = 7)	

the adult-sized male in Group P (03) replaced the breeding adult male (LE) in singing at the end of the song rather than only at the beginning. In all groups the two adult (Ad) individuals figured prominently in all songs, but only the adult female always sang throughout the group's song.

Group P (Analamazoatra). The adult female normally called throughout the song. All individuals roared, but the youngest individual (01) followed this up with one or two calls only or remained silent. The subadult (02) usually sang more than 01, joining in at the *beginning* or, occasionally, the middle part of the group's song. The alternating roles of the adult male and 03 in Group P's calling pattern were of great interest due to their change during the course of the study. One characteristic feature of the adult male's singing pattern was his distinct contribution at the beginning of the song, a low-pitched howl (Type 1). The adult male initiated the communal roar in 60% of the songs monitored closely for the timing of individuals' calls. Furthermore, during the first 9 months of the study the songs always ended with only the adult breeding pair calling. Between the end of February and July of 1973, however, 03 replaced the adult male in this terminal "duet" with the adult female. The adult male and 03 were never seen to call at the same time during the song. Duetting with the adult female therefore occurred intermittently and exclusively by the two oldest males; when one started the other stopped, or after one had stopped the other soon started.

Group P1 (Analamazoatra). A group ranging within part of the 1972/1973 Group P territory was found in July 1984 to consists of an adult female with an infant, and adult male, and an adult-sized individual. The latter two were distinguished by the former's large

Table III. Individual Call Rates in Group P and Group V from the Analysis of a Single Song from Each Group

				♀		♂	
Date	Group	Song duration (sec)	Overall call rate (calls/sec)	No. calls	Call rate (calls/sec)	No. calls	Call rate (calls/sec)
27.11.72	P	142	0.57	37	0.26	32	0.22
26.10.72	V	95	0.57	32	0.33	21	0.22

testicles, subordinate behavior to the female, and low position taken in trees (Pollock, 1979a). On the three occasions when individuals' participation could be determined, the adult-sized individual (later sexed as male) sang only at the end of the song, when the adult male had finished accompanying the female. The adult female sang throughout. Despite their apparent habituation to the human observer and the adult pair's physical resemblance to 03 and 01, no individuals could be recognized with certainty as belonging to the former Group P.

Group V (Analamazoatra). All members roared, including the infant from a very early age, but only the adults continued. The adult male began with characteristic long, low howls (Type 1; Fig. 4) of a fundamental frequency of 800 Hz, each lasting 3 sec, while the adult female produced Type 2 and Type 3 calls at a high rate. Both animals started and ended together.

Group IV (Vohidrazana). All animals roared in this group. On the one occasion that individuals' singing order was established without doubt, the adult female sang throughout and ended in duet with the oldest (probably female) offspring. In two further songs analyzed by tape three voices were detected singing until the end.

Most songs from groups living close to the main study groups had a structure similar to that of Group P and V, where the difference between adult male and female was distinct. This observation supported census data indicating that *Indri* groups always contained an adult pair and also suggested that, within each group, *Indri* song patterns have the following consistent characteristics.

(i) Only adult females call for the duration of their group's song, but the individual most commonly starting the song is the adult male.

(ii) Young animals aged from 1 to 3 years participate only in the introductory roar or the very first second of the rest of the group's song.

(iii) Subadult (age 3–6 years) *Indri* may continue to sing for part or all of the first half of the group's song; adult-sized group members may sing to completion.

(iv) The type of call emitted (see below) and the timing of individuals' contributions differ; the adult female never calls alone during the song but other adult-sized group members differ in the timing of their contributions.

Song Patterns in *Indri*

Temporal Distribution

An observer in a forest inhabited by a substantial *Indri* population hears either a single song emitted by one group or a series of songs, some overlap-

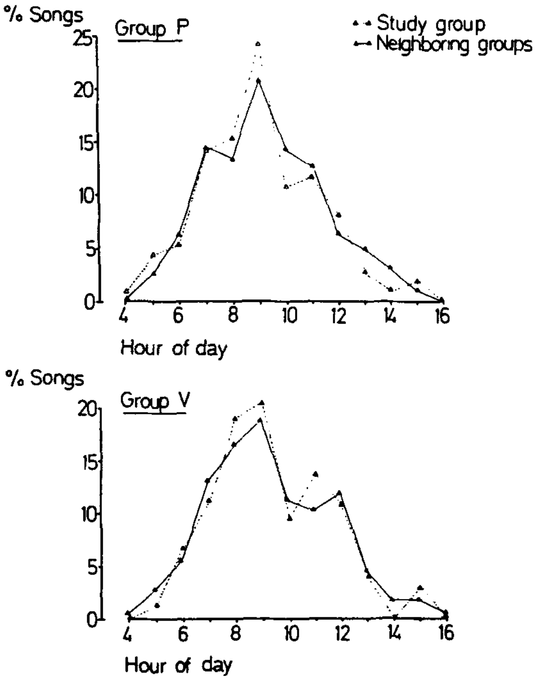


Fig. 5. Hourly distribution of *Indri* songs throughout the year by the study groups and their neighborhood groups.

ping in time, given by several groups (song clusters). Quiet periods both precede and follow a song cluster.

Over the whole year *Indri* songs are distributed in an approximately normal fashion about a mean of 0900 hr in each study area (Fig. 5). As singing by *Indri* groups induced other groups to reply, the samples of singing times are not independent of each other within any specified time period and therefore cannot be statistically compared. The songs were, in all areas, confined largely to the morning.

An analysis of song clusters was made because of the possibility that they reflected a unit of communicative interaction within the population. A song was considered to be part of such a "cluster" of songs if it (a) overlapped the song that started it; (b) started immediately after the preceding song ended, allowing time for sound transmission; or (c) started within 10 sec of the end of the preceding song. The 10-sec limit, beyond which subsequent songs were defined as belonging to a different cluster, was a natural one. The first songs of a new cluster generally commenced a few minutes or even hours after the last song of the preceding cluster defined in this way.

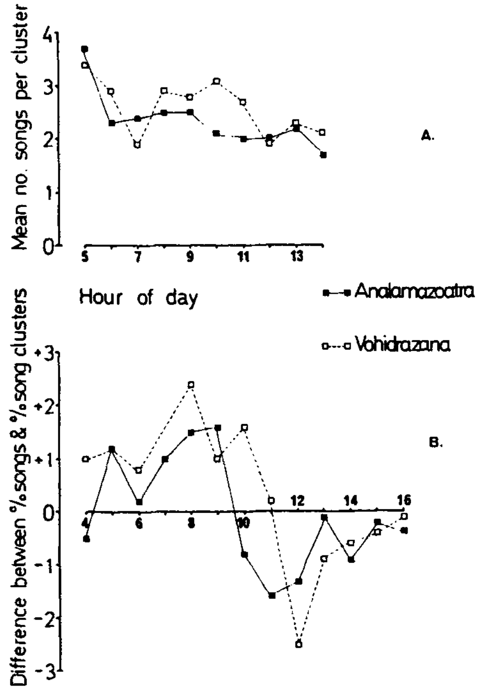


Fig. 6. Hourly distribution of groups of songs (song clusters) throughout the year. (A) The mean number of songs in a group of songs is illustrated for Analamazoatra and Vohidrazana. (B) The differences between the percentage of songs and the percentage of groups of songs are shown for each hour of the day at Analamazoatra and Vohidrazana. Positive values indicate a preponderance of song clusters containing few songs.

The temporal distributions of song clusters measured by the proportion of calls heard daily that occurred in each hour of the day followed the pattern for all songs and did not differ among the three study areas.

A definite tendency for songs to occur in larger clusters in the morning than in the afternoon was present, however, at both Analamazoatra and Vohidrazana (Fig. 6A). Furthermore, songs emitted very early or very late in the day were less likely to be "answers" or be "answered" than songs emitted in between (Fig. 6B).

Seasonal Variation

The frequency and timing of *Indri* songs vary seasonally. The two main study groups sang at least once each day for the same proportion of days

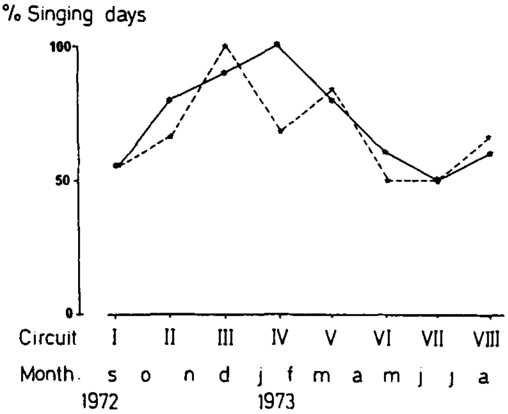


Fig. 7. Seasonal distribution in the proportion of days of which the two main study groups sang. Solid line, Group P; dashed line, Group V.

overall; but this proportion increased gradually as the study progressed, peaking in the midsummer period (Fig. 7). This period (December and January) is characterized by more frequent singing by each group [up to 6 songs emitted per group each day (Pollock, 1975a)], starting earlier in the morning and continuing later in the afternoon. Songs were not infrequently heard at night in December 1972 and visits were made at night to the study groups' sleeping trees to confirm that they were not active at this time. December and January are the months of greatest general activity for *Indri* and breeding behavior was observed in these months. Differences between the groups in the timing of the highest singing frequency (Fig. 7) were due either to reduced singing in Circuit IV (midsummer) by Group V during a 4-day cyclone that affected all activities or to the large number of "cohesion songs" emitted by Group P while the adult female was injured (see below).

The frequency of songs emitted from groups in the neighborhood of Group P differed from the frequency of those in the neighborhood of Group V. The numbers of songs by *Indri* groups near Group V exceeded those near Group P (Fig. 8) at times of a high overall singing frequency but not at other times of the year. There was no reason to consider the observer's auditory perception to be superior or the animal density greater around Group V's territory than around Group P's, and the difference is not understood. The singing frequency was too variable between days for the seasonal distribution of songs to be compared in the other two study areas, which were each visited only for 3 days every 6 weeks. The same seasonal trends appeared to be present, however.

Songs started earlier and continued later in the austral summer (Circuits III and IV), when most songs were heard and *Indri* were active longest (Fig. 9). No simple relationship existed between the time of onset of groups'

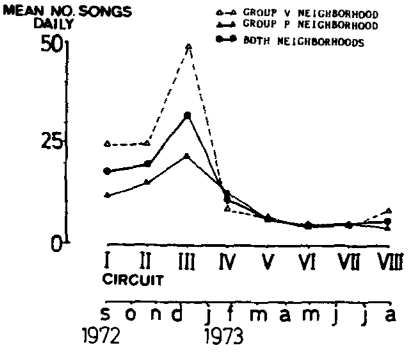


Fig. 8. Seasonal variation in the mean number of songs emitted daily by local populations surrounding each main study group at Analamazoatra.

songs from the population and the time of onset of songs from the study groups themselves.

Song Cluster Size

The two study groups did not differ in their involvement in song clusters of various sizes (Fig. 10) [χ^2 (3 df) = 6.208; $0.1 < P < 0.2$], but their respective neighboring groups did [χ^2 (3 df) = 7.895; $0.02 < P < .05$]. This difference could be attributed to the proportion of songs that were not answered and not themselves answers, i.e., single songs [χ^2 (1 df) = 5.022; $0.02 < P < 0.05$]. There appeared, therefore, to be more "two-way" communication among the groups surrounding and near Group V than among those

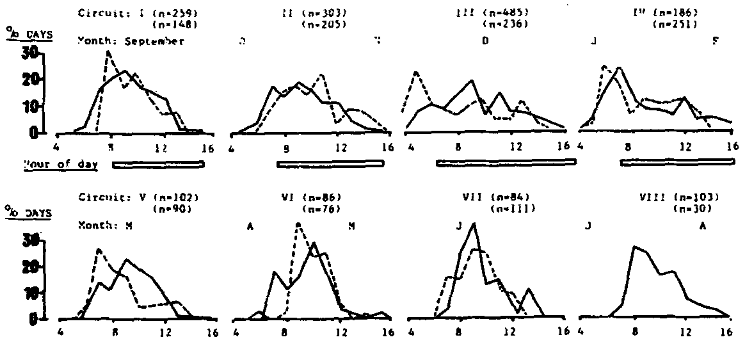


Fig. 9. Seasonal variation in the hourly distribution of songs at Analamazoatra and Vohidrazana, and mean duration of activity period of Group P (open horizontal bar).

Table IV. Daily Variations in the Number of Songs Heard at Analamazoatra (The Superscripts Refer to the Number of Songs Emitted by Study Groups)

Observation day No.	Circuit												Totals
	I		II	III		IV	V		VI	VII		VIII	
	S[a]	O	N	D	J	F	M	A	M	J	J	A	
						(1) Group P's neighborhood[b]							
P11	–		14	35		12	–		1	25^{4}		4^{2}	
P10	–		22^{2}	21^{1}		9^{2}	3^{1}		11^{2}	10^{1}		2	
P9	–		13^{1}	26^{2}		12^{3}	9^{2}		4	3^{1}		6	
P8	–		7^{1}	31^{3}		10^{2}	3^{1}		9^{2}	5		6^{1}	
P7	14^{1}		3	26^{7}		21^{4}	10^{1}		8^{1}	1		7^{1}	
P6	14^{2}		26^{2}	12^{2}		19^{4}	6^{2}		9^{2}	1		3^{1}	
P5	11^{1}		19^{2}	13^{2}		10^{2}	5^{1}		2	4^{1}		8	
P4	9^{1}		21^{2}	18^{3}		7^{3}	12^{1}		1	1		10^{2}	
P3	14^{0}		17^{3}	23^{2}		16^{4}	12^{2}		5^{1}	2		7^{1}	
P2	9^{1}		9^{1}	16		12^{4}	3		7^{3}	5^{1}		1	
Total	71^{5}		151^{14}	221^{30}		128^{28}	63^{11}		57^{11}	57^{8}		44^{8}	792^{115}
% contribution by Group P	7.1		9.3	13.5		21.8	17.5		19.3	14.0		18.2	14.5
						(2) Group V's neighborhood[c]							
V7	58^{4}		33^{4}	25^{3}		11^{1}	4^{2}		7^{2}	4		14^{1}	
V6	14		24	55^{3}		14^{1}	9		2	10^{1}		3	
V5	25^{1}		31^{2}	57^{4}		9	4^{1}		2	2^{1}		11^{3}	
V4	15^{2}		38^{3}	64^{5}		7^{1}	8^{1}		7^{2}	6^{1}		3	
V3	26^{3}		20^{1}	57^{5}		3	11^{3}		4	3		15^{2}	
V2	9		3	36^{3}		10^{1}	4^{2}		4^{1}	6		4^{1}	
Total	193^{11}[d]		149^{10}	294^{23}		54^{4}	40^{9}		26^{5}	31^{3}		50^{7}	837^{72}
% contribution by Group V	5.7		6.8	7.8		7.4	22.5		19.2	9.7		14.0	8.6

[a] Month.

[b] Mean number of songs per day: Group P, 1.5; Group P neighborhood, 10.3.

[c] Mean number of songs per day: Group V, 1.4; Group V neighborhood, 16.7.

[d] Eight days' data.

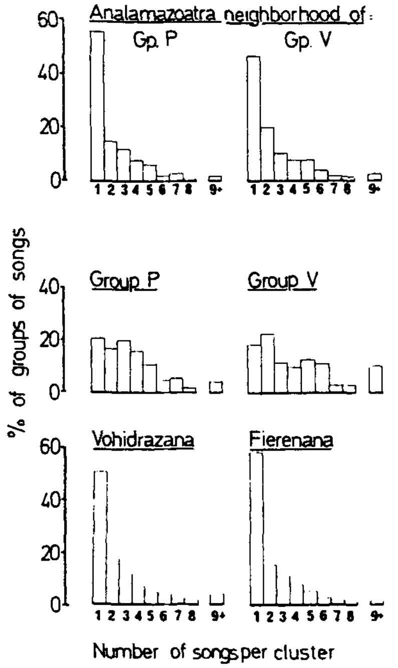


Fig. 10. The proportion of songs by each study group, by groups in their neighborhood, and by groups in other study areas that occurred in song clusters of different sizes.

near Group P. It is perhaps relevant that the former lived primarily outside the Special Reserve and in an area containing small *Eucalyptus* plantations, i.e., in a more disturbed habitat.

Song cluster sizes were not directly comparable among study areas, as the sensitivity to distant songs varied according to the position of the observer.

Daily Variation in Singing Frequency

The number of songs heard within each 6-week observation period varied widely from day to day (Table IV). To some extent this depended on the weather: cold, wet, and windy conditions appeared to inhibit calling. On days with sporadic, hard rain, *Indri* would move, feed, and sing between showers. For *Indri* in the neighborhood of Group P, the effect of rain was investigated by dividing up observations of singing frequency into (a) dry days (rain fell 0–5% of the time), (b) slightly wet days (rain fell 12–30% of the time), and (c) very wet days (rain fell at least 37% of the time). The results (Table V) show that heavy rain (or conditions associated with it) affect the number of songs emitted each day and the mean number of song clusters

Table V. The Association Between Rain and Singing Frequency for Groups at Analamazoatra

	Dry	Slightly wet	Very wet
Sample	15 days	14 days	10 days
No. songs/day	12.7	12.3	7.7
No. clusters/day	5.5	5.2	3.4
X songs/cluster	2.3	2.4	2.2

but not the mean number of songs in each cluster. The mean number of songs did not, however, reduce in proportion to the amount of time that rain fell, as *Indri* compensated by singing relatively more during bright intervals in the weather.

The two study groups at Analamazoatra did not differ in the number of days on which they sang at least once ["singing days;" $\chi^2(1\ \mathrm{df}) = 0.509$; $0.3 < p < 0.5$], nor did the numbers of songs they emitted daily differ greatly (Fig. 11). The mean singing frequency on Group P observation days was 1.51 songs/day; that of Group V was 1.29 songs/day. The mean number of songs emitted on singing days was very similar in the two groups: 2.05 (Group P) and 1.94 (Group V).

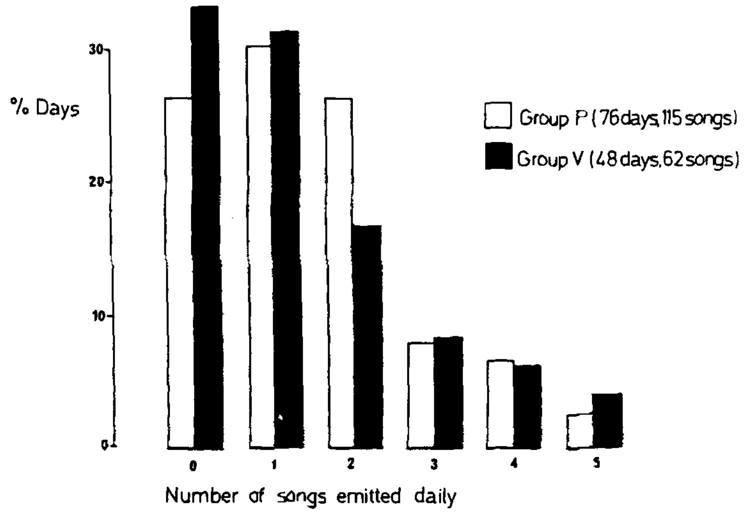


Fig. 11. The proportion of days on which different numbers of songs were emitted by the two main study groups at Analamazoatra.

The Duration of Indri *Song*

A single *Indri* song may last from 40 sec to over 4 min. Group P sang, over the year, each time for a mean duration of 141 sec ($N = 107$), whereas Group V sang for a median duration of 100 sec ($N = 81$). The distributions of song duration of the two main study groups are quite different (Fig. 12), with Group P singing for periods of time that were much more variable (SD = 4.78 sec) than Group V (SD = 2.29 sec), as well as singing longer songs.

The possibility that song duration related to group size in *Indri* was therefore tested in each study area by comparing the song duration in groups in which at least three voices were heard to that in groups in which only two voices could be distinguished. The results (Table VI) proved that in every case the longer songs were emitted by groups with more individuals (i.e., larger groups) singing.

Mean song durations in the three study areas were similar. Due to the inclusion of the relatively very long songs of Group P in the sample from groups in the neighborhood of Group V (the two study groups had adjacent territories), their longer mean song duration cannot be meaningfully compared. The mean song duration at Fierenana (80.0 sec, $N = 188$) was significantly lower than that at Vohidrazana (89.9 sec, $N = 483$; $t = 4.04$; $P < 0.001$) and that of groups surrounding Group P (91.7 sec, $N = 296$; $t = 3.66$; $P < 0.001$), but those at Vohidrazana and Analamazoatra did not differ ($t = 0.62$; $0.5 < P < 0.6$). The significance of this result is probably explained by the preponderance of small groups at Fierenana, where all six groups censused consisted of one adult pair and infant. The song durations of small groups in all study areas were similar to those at Fierenana, but the duration of songs by Group V, of identical group composition to all groups censused at Fierenana, was consistently longer despite similar variances. It appears, therefore, that song-length variation exists between groups of similar sizes.

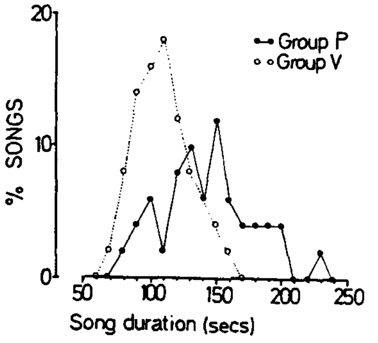


Fig. 12. The duration of songs in seconds of each study group at Analamazoatra throughout the year.

Table VI. Group Size and Song Durations

Study area	2 animals	3 animals	*t*	*P*
Vohidrazana				
X	79.1	120.7		
SD	22.1	42.0		
N	59	47	6.49	<0.001
Fierenana				
X	78.8	115.1		
SD	20.8	30.6		
N	25	14	4.29	<0.001
Analamazoatra (excluding 1972/1973 study groups)				
X	78.0	118.1		
SD	20.4	32.3		
N	29	19	5.14	<0.001
Study groups				
X	98.5	197.5		
SD	20.9	45.6		
N	32	32	5.34	<0.001

Furthermore, differences between Fierenana and other study areas in the duration of *Indri* song could not result from seasonal changes in song duration, as data were collected equally in all areas throughout the year and the song duration did not vary substantially within study areas at different times of the year (Pollock, 1975). It seems unlikely that local differences in the weather were responsible for differences among areas in song duration, as rain was seen to have no effect on the length of *Indri* song within a study area (dry versus very wet: $t = 0.14$; $0.8 < P < 0.9$).

In 53 (91%) of the 58 instances that Group P's songs occurred in clusters, they sang the longest. Although most of Group P's normal songs were longer than "group cohesion" songs (see below; $P < 0.001$), the other 5 songs were judged to have been used for intragroup aggression purposes. All normal songs from Group P, therefore, were longer than other normal calls. The group's complement, five animals, was also more than that of any other *Indri* group seen in any study area.

The Function of *Indri* Song

Introduction

Loud calls have been interpreted by many authors as a mechanism of self-advertisement essential to territorial defense (Marler, 1965; Andrew, 1972; Buettner-Janusch, 1973; Tembrock, 1974). Regular loud calls, which may be heard for over 1000 m, are emitted by many primates including titis, mangabeys, colobus, howlers, gibbons, and siamang, in addition to several lemur species (notably, *Varecia variegata* and *Indri indri*). As a rule, these calls are emitted early in the morning or during the first hours of the activity period and may be instrumental in inducing members of groups to confront each other at territorial borders (Ellefson, 1968, 1974; Robinson, 1979). They either may evoke no recognizable changes in behavior or may result in increased separation of groups (Chivers, 1969; Waser, 1975). In all cases a function in intergroup spacing has been attributed to the behavior and ecologists have been quick to point out that this may result in a more even pattern of environmental exploitation.

In discussing the "territorial" function of loud primate calls, careful distinctions have rarely been made among the following contingencies:

(i) advertisement of "self" so as to warn conspecifics of presence;
(ii) delineation of territory by border-region definition; and
(iii) communication of possession or occupation of an already defined territory. ("Territory" is here assumed to be of permanent geographical situation over the period to be considered.)

Additional information mediated by loud calls may be classified into three divisions.

(i) Information about the environment, e.g., food, predators, and weather.
(ii) Information about the dispersion and distribution of individuals or groups, e.g., location, distance, or direction of individuals. This may include additional information about the activity of individuals or groups at a particular location.
(iii) Information pertaining to the characteristics of the calling animals, e.g., age, sex, reproductive condition, and group size and composition.

In the following discussion the possible function(s) or "areas of function" of *Indri* song are tested from information obtained during the present study.

Territoriality and Associated Functions

Influence of Song on Ranging Behavior. No influence of song on everyday aspects of ranging behavior could be determined. The direction of movement taken by study groups after songs were emitted by groups within 1000 m was recorded for those times of the year when vocal activity in the population was high (summer) and when it was low (winter). The quadrats (50 m-sided squares) entered following such calls were divided into those representing either an increase or a reduction in the distance between the study group

Table VII. Direction of Movement by Group P in Response to Songs Within 1000 m in Two Seasons*

Movement	Nearer to song source	Further from song source	Total
High	17	19	36
Low	8	9	17
Total	25	28	53
%	47	53	100

*χ^2 (1 df) (overall) = 0.0001; $0.98 < P < 0.99$.

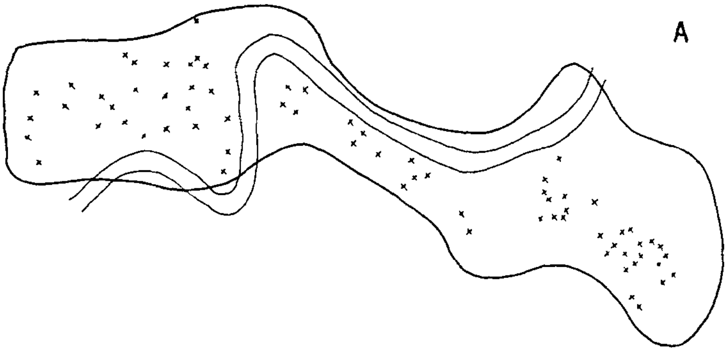
and the singing group. Following the analysis no distinction between such quadrats could be determined (Table VII).

Territory Definition. Sound-attenuating properties of the environment derive from many sources and are complex and variable in their effects (Morton, 1975). As "distance" may be inaccurately communicated through highly sound-attenuating media, the definition of a territory may not be precisely communicated to distant groups. Calls emitted from (a) peripheral locations or (b) throughout the territory might therefore be expected to transmit such information primarily to groups nearby.

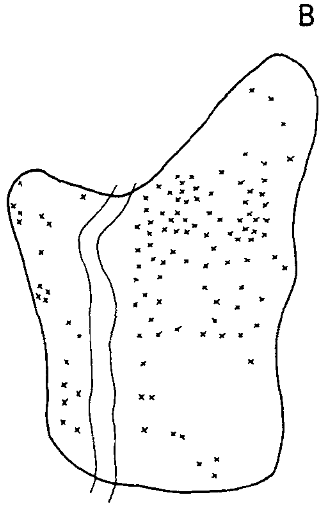
Indri in this study did not *demarcate* peripheral locations by singing. They called from any part of their territory (Fig. 13) apparently in the same proportion to the amount of time they spent there. The precise relationship between quadrat use and singing location could not be examined statistically, as there were too few songs emitted from too many quadrats.

Over considerable periods of time (maximum observed rate, 1.5 calls/day) an even pattern of song emission throughout all parts of a territory could define that territory to nearby groups if *Indri* could differentiate among groups by characteristics of their songs. There is no proof that this occurs, although there is sufficient variation in song parameters for the experienced human observer to distinguish some groups. Alternatively, the declaration that the certain part of the environment is occupied, no matter by whom, may be functionally pertinent to the singers and the receivers.

Territory Occupation. Visual contact between neighboring groups may have been more substantial than was apparent to the observer on the ground. Furthermore, *Indri* groups relatively rarely reacted to neighbors' songs (see below) and the song was therefore considered to be of greater significance to groups in the near-distance than to territorial neighbors. The region of issue of a song more closely approximates the occupation of a whole territory to distant than to nearby groups. Several such signals could transmit information about gross measures of population density or population or group structure in a quite distant part of the forest. This feature may have been aided by the tendency for both study groups to sing following a song



Group V



Group P

Fig. 13. Singing sites for *Indri* study groups at Analamazoatra. Each cross marks the spot at which the two main study groups sang within their territory in the course of all-day follows. A, Group V; B, Group P.

from groups situated relatively near to them, although no other change in their behavior was evident (Fig. 14).

When the geographical locations of songs that were replied to were examined, it was apparent that Group V was responding mostly to calls from a specific border region (Fig. 15a), while Group P was not (Fig. 15b). In this case, however, this was possibly due to the distribution of surrounding *Eucalyptus* plantations (which do not permanently support an *Indri* group) rather than a preferential pattern of response.

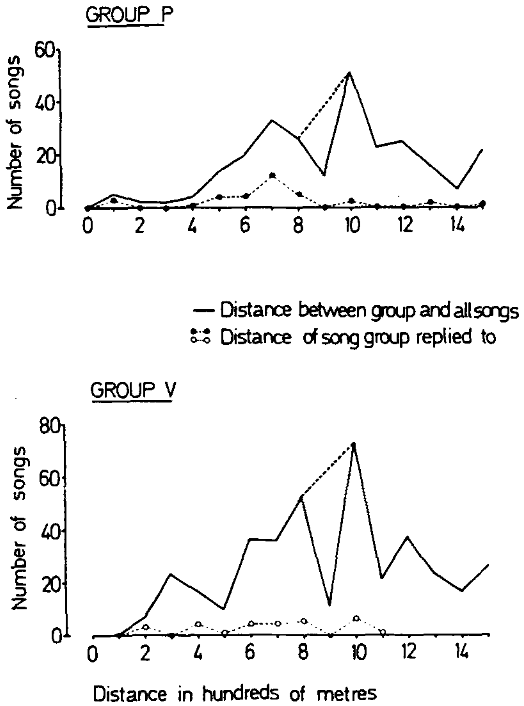


Fig. 14. Distances between study groups and groups whose songs they replied to, compared to distances from the group to all songs heard in the vicinity.

Territorial Defense. When two *Indri* groups approach each other at a common territorial border, intense displays of movement and singing take place. Although only eight border encounters were fully observed during the course of the study, these appeared to be of two main types.

(1) Border encounters which occur when two groups fortuitously range at the same time in the same border area (Type A; four cases observed).

(2) Border encounters which occur when one group sees or/and hears a neighboring group at, or even just *inside*, the territorial border when the group is centrally located (Type B; four cases observed).

Indri territories partition the forest to a large extent into group-exclusive portions. Surrounding each territory is a narrow band (in the three cases where this was measured, it varied from 30 to 50 m in width) of common land. This common land was normally used for ranging and feeding activities by each group; in the three cases observed, only two groups shared this area (Fig. 16) in their daily activities. On reaching its outer ranging limit, an *Indri* group *always* turned to a central or tangential direction of travel. On four occasions *Indri* groups were seen to meet, following apparently normal

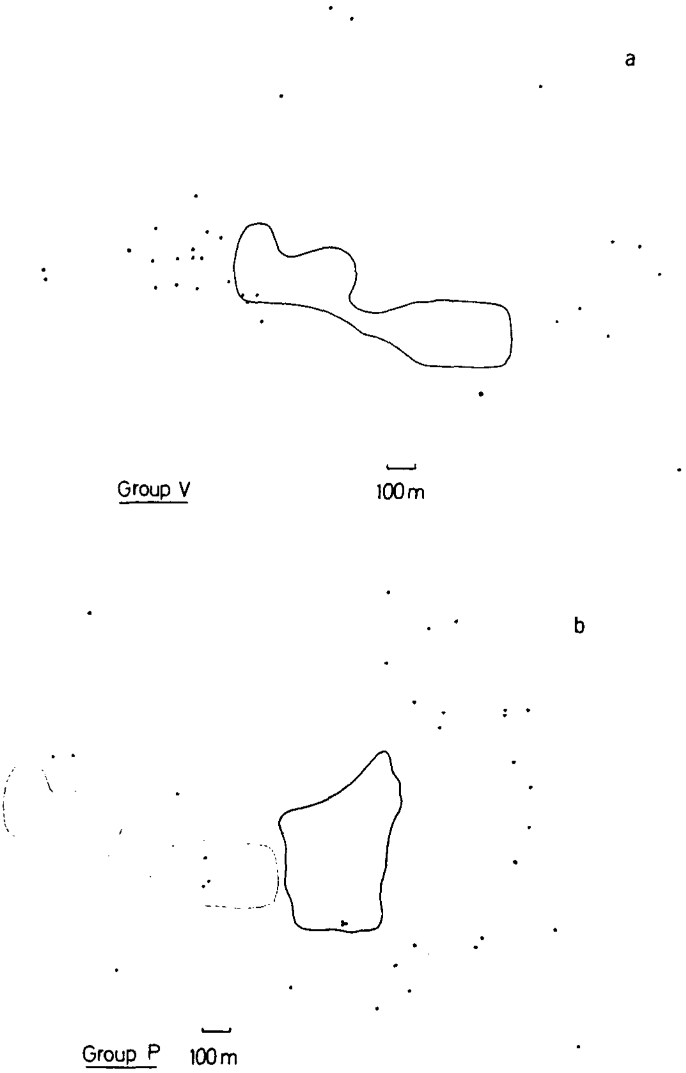


Fig. 15. The location of groups whose songs were "answered" by Group V (a) and Group P (b) over 1 year. Each spot marks a singing group, but because study groups must have answered the same group on different occasions, each spot does not represent a separate group.

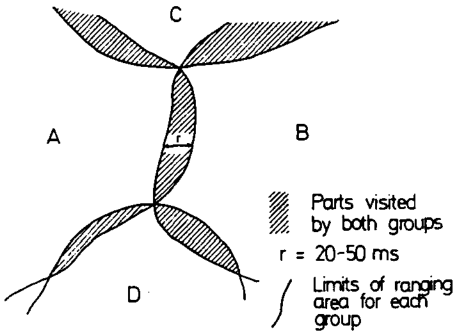


Fig. 16. Diagrammatic representation of border regions between neighboring *Indri* groups.

ranging patterns, in an area of common land. No strange or anticipatory behavior was seen in the period preceding the encounter. For Group P such an event occurred on 22 November 1972:

0835 Single HOOT [alarm call given to a terrestrial disturbance, such as a human observer] by an individual from the neighboring group (N) in the border region 150 m from Group P.
0845 Returning to Group P, I find them motionless, resting quietly.
0911 One member of Group P jumps, 36 min after the first HOOT.
0918 The adult male (P) moves off in the direction of group N and cheek-marks.[3]
0924 The adult male (P) genital-marks[3] and moves along the border region toward Group N.
0928 Both groups suddenly roar simultaneously and Group N sings, 20–30 m away from the adult male (P). Group P replies halfway through Group N's song, the adult male (P) singing some distance from the rest of his group. The adult female (P) sings very loudly. A Group 300–400 m away then replies to Group P, and with the adult male returning to his group, Group P sings again. The pattern of singing is very complicated and different from the relaxed morning calls. There is a lot of animal movement during the calls from both groups. The adult male defecates while singing.
Group N then replies to Group P and this is followed by a call from Group V, 600–700 m away.
0942 The calls end after a distant group sings about 1000 m away to the northeast. Group P had been singing for approximately 9 min continuously.
0955 After more songs from Group N and Group P they start to move in opposite directions (Fig. 17).

Similar patterns of singing and movements were observed in Group V, in Group IV, and in an unhabituated group at Analamazoatra. During all these encounters the adult males of each group appeared to be the closest together. It is not impossible that physical combat occurred; the Group P adult male had most of one ear missing and one adult male (Group U) had lost his right eye.

Type B encounters were probably more common than Type A encounters. During census walks, the observer frequently encountered unhabituated

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[3] Forms of scent-marking behavior.

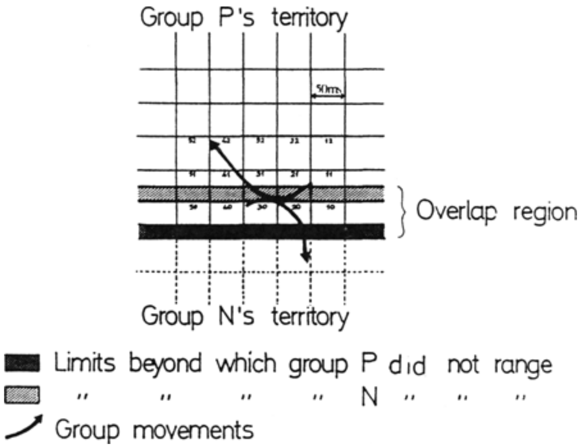


Fig. 17. The movements of Groups P and N during a border encounter on 22 November 1972 (see text).

Indri in strange group configurations: groups of two or three animals separated by some distance from one other animal. Retrospective analysis of the singing patterns indicated the presence of not one but two groups of *Indri* in these locations. On 6 March 1973 observations of Group V led to a classification of these group configurations. A neighboring group sang from well inside the Group V border region, some 250 m from the resident group. The adult male of Group V immediately left the adult female with infant after they had replied and leapt off to the border region. Once there he started to sing and was accompanied as usual by the adult female despite their wide separation. A succession of alternate songs from the two groups ensued, with the invading group farther and farther away on each occasion. After an additional 30 min, the adult male returned to the female and normal ranging and feeding activities ensued. There were many calls in the population where a singing pair of *Indri* appeared to be widely separated, and it is probably that on these occasions the adult male was confronting a neighboring group. The temporal integrity of the group's song in these situations, however, remains complete.

Territorial "defense" of the two types described above was rarely witnessed, and these observations may constitute extreme examples of more common forms of interaction between specific groups. A very common observation, for example, was a simple vocal interaction between two groups, usually from 200 to 400 m apart, singing in an A-B-A pattern, the group singing first also ending the interaction. When groups were very close the repetitions could be continued and prolonged: A-B-A-B or A-B-A-B-A, etc., grading continuously into the patterns described above where visual confrontation is also present.

There was no evidence from observations of the study groups that seasonal increases in singing behavior resulted from a greater incidence of these types of calling sequences; but a further examination of whole populations (Vohidrazana and Fierenana) was made in order to confirm this, as it was considered possible that seasonal changes in the tendency to range near the border regions could be of ecological significance. A mean of 12.2% of the songs at Vohidrazana was found to be in the A-B-A format, and 12.4% of the songs recorded at Fierenana also occurred in this pattern. The percentage of these songs did not increase dramatically at any particular time of the year (Fig. 18), but a peak in the summer (cyclonic weather may have interferred with data collection in Circuit IV) might be suggestive of increased border ranging behavior at that time. It also appeared that these types of songs may have occurred more often early than late in the morning, although at Vohidrazana, where the data are most complete, this variation proved to be statistically not significant [χ^2 (1 df) $= 3.194$; $0.05 < P < 0.01$].

Another property of the population's singing behavior was the unequal geographical distribution of singing activity at Vohidrazana, the only study area where such positional heterogeneity was evident because of the large number (about 40) of groups that could be heard from one observation position. In order to examine the presence of "hot spots" in the population which could not be attributable to only one or two vocal exchanges, the proportion of songs deriving from different sectors of the forest was analyzed. Only those parts of the forest which could be viewed (and which were thus attenuating sound by only a single tree-canopy layer) were considered. Song frequencies from the northern and southern sectors were compared by a sign test and found to be significantly different ($P < 0.001$). Each segment of 10° was then examined by a Friedmann one-way analysis of variance and found to be significantly variable [χ^2 (12 df) $= 35.93$; $P < 0.001$]. It is not possible to determine whether these areas of high calling activity contained

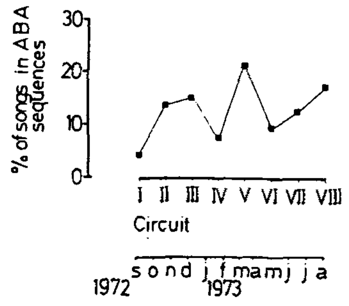


Fig. 18. Seasonal variation at Vohidrazana in the proportion of songs classified as A-B-A sequences.

calls of a specific format, pattern, or duration, but there was no preponderance of obviously distinct songs. It is possible that *Indri* territories vary somewhat in size and that in areas of a higher population density, different (more frequent) calling behavior may be required by groups to defend their territories. Alternatively, hot spots may signify areas of territory formation or reformation, a contingency that requires further study.

The role of *Indri* song in territorial behavior appears to be complex. In all probability songs are not an influential parameter in normal ranging behavior, but when groups are near to each other, they could induce movement and confrontation. It is important to recognize that, in addition to performing a central role in intergroup encounters, songs were also emitted in relaxed morning exchanges with groups up to 1100 to 1200 m distant (or more) on 2 of 3 days. In these cases it is possible that singing remains functionally related to communication with hearing groups but is in actuality largely redundant because of a wide separation of groups.

Group Cohesion

Occasionally members of Group P would become dispersed, splitting into a pair and a trio or into even smaller subgroups. If this dispersion resulted in independent ranging of individuals or pairs separated by over 100 m, the effect of *Indri* song was reaggregation. In such contexts, the song, although similar in structure and volume to morning songs, differed from them in four ways.

(i) It could be initiated by any individual.

(ii) It was performed at a slower tempo and for a shorter duration.

(iii) It contained silent intervals that might last for several seconds.

(iv) It possessed no consistent pattern, any individual singing at any time. Usually only one animal sang at a time.

The song was judged to be cohesive in function when these characteristics and the relevant context with subsequent aggregation of animals were present. During reaggregation, some animals remained stationary and the others moved toward them. How it was established which animals should move and which should wait remains undetermined. On one occasion, however, all individuals moved and subsequently met at a dense food source.

Cohesion songs often, but not always, contained a "roared" introduction—as did most songs. Sometimes the roar sufficed for contact to be reestablished, and in these cases it appeared that the song was dispensed with or was very short.

For Group P, 23 of the 114 songs emitted while under observation (20.2%) were judged to have been cohesion songs, and these were confined mostly to Circuit IV. At this time the adult female, nursing a wound in the lower back, which made movement difficult, stayed alone in the central part of the group's range, while the other group members ranged normally. Each afternoon a song by the whole group resulted in reaggregation at the female's resting site. During the other circuits, only 7% of the songs were considered to have been made for cohesion purposes, whereas during Circuit IV, 61% were so judged.

Nonterritorial Aspects of Intergroup Communication in Indri

Indri song appeared sometimes to be induced by potential predators or disturbances—e.g., birds of prey, airplanes, thunder, the observer (for unhabituated groups)—and could therefore have conveyed information about such events to conspecifics and, perhaps, to other species. No difference from normal vocalizations was apparent in the structure of these songs.

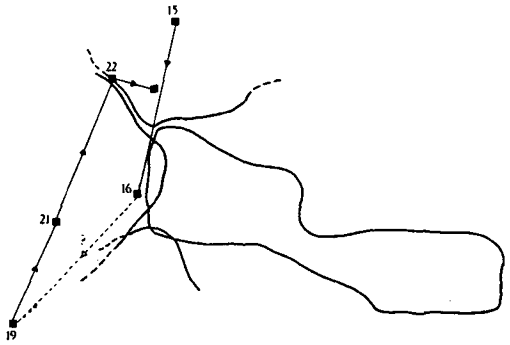
In addition, the patterning of the songs of Group P—the asynchrony of the adult male and 03 in singing with the adult female—was so disciplined as to suggest it to be a property of *Indri* (rather than an idiosyncracy of Group P) and, possibly, of communicative importance. It is conceivable that, together with other properties of this group's songs (e.g., duration and young-animal participation), this pattern may have communicated details of group composition and the constituents' ages and sex to other groups.

Mate Location

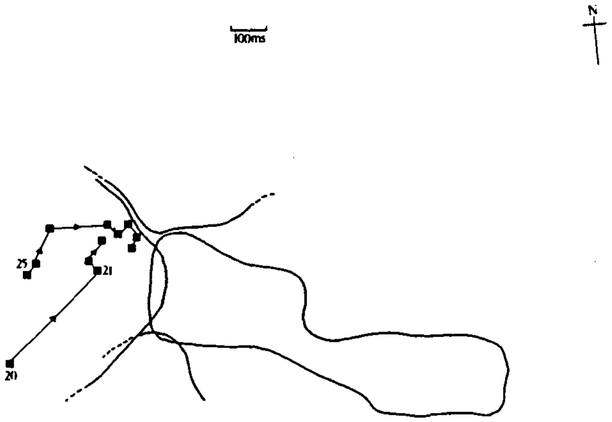
During the month of September 1972, one individual *Indri* ranged over the territories of two or three groups adjacent to Group V. This animal's characteristic and unique "screaming" songs enabled plots to be made of its positions while Group V was under observation (Fig. 19). The song was marked by sequences of Type 1 calls, which are emitted only by males. The animal was known to range alone, as it was found by chance during a nocturnal survey, sleeping near the ranging limits of three *Indri* groups.

The songs from the same individual in October 1972 showed that it had probably restricted its ranging to one territory, part of whose limits had been previously established by another group.

The nonterritorial pattern of movements of this individual, which eventually moved away from the area or disappeared, preceded the mating season by 1 or 2 months and may therefore, have been concerned with the acquisition of a breeding partner. In July 1984 a male with identical vocal characteristics was heard several times singing with a female, from an area approximately 2.5 km from where it was last heard, in a normal group song.



SEPTEMBER



OCTOBER

Fig. 19. Nonterritorial ranging in *Indri*. The singing locations of and adult male *Indri* in September and October 1972, with known territorial borders of four groups marked. Numbers refer to days of the month.

Attempts to find his group failed, but it seems very likely that this lone male had eventually located a mate and established a territory.

The ability to monitor the composition of other groups may be of great importance in pair-bond formation for slowly maturing, family-living animals with birth seasons separated by long intervals. If mate location is a problem for *Indri*, the approximate position of another individual of the opposite sex and the right age may be advertised by this means, and scanning large numbers of groups over some time may inform a maturing offspring that mates are available in certain areas, obviating the need for close, perhaps dangerous, physical contact with many groups.

Strictly territorial species, furthermore, obtain direct demographical information about close neighbors only during physical encounters—which, in the case of *Indri*, are very infrequent.

The process by which new *Indri* groups are formed remains conjectural. The possible presence of individuals (probably males) that range across other groups' territories has already been discussed. *Indri*'s reproductive strategy, with a long maturation period (5-8 years) and infrequent singleton births at 2- to 3-year intervals, must focus on high-quality offspring (Pollock, 1979a). It is possible that in such *K*-selected cases deleterious homozygosity can be avoided only if newly adult animals range considerable distances to locate mates. In these cases, the ability to determine which regions with a low group density contain suitable breeding partners may confer an advantage. For siamang, however, similar observations of a lone male calling prior to territory occupation occurred just outside the boundaries of the parental group (Aldrich-Blake and Chivers, 1973), and similar adjacent patterns of residence have been reported for *Hylobates klossi* (Tenaza, 1975; Tilson, 1981).

DISCUSSION

The complexities involved in determining the function of primate loud calls from naturalistic studies have led many observers to be satisfied with unitary explanations. Functional multiplicity is, however, a real alternative, especially where the species' behavioral repertoire itself or its control or organization in the brain is relatively limited.

Loud calls have been assumed not only to function in territoriality—more specifically, territorial defense—but to define the area itself (Marshall and Marshall, 1976). In all species of contagiously calling primates, active territorial encounters in "border regions" occur, and calling is a dominant activity in these situations. However, truly territorial primates have been found to stay within their territorial boundaries in the course of their daily ranging activities irrespective of their calls or the calls of their neighbors.[4] They may additionally call rarely enough to permit substantial transgressions should calls be the only mechanism ensuring territorial integrity. The most frequent hylobatid caller is the agile gibbon, at an average of 2 calls/day, with lar gibbons and siamang calling, respectively, 1 call/day and 1 call/3 days (Chivers and Raemakers, 1980).

Do primate loud calls generally function to separate groups and do such calls accompany, maintain, or define territorial existence? While determin-

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[4] A dogma of the opposite kind is implied by Byrne (1982) in declaring that because siamang call from the "territory" center and boundary conflicts were rare, they may not be territorial.

ing a common pattern of dispersion, Marler (1968) recognized that aggression followed in some circumstances of loud-call emission in primates, and Wrangham (1977) has highly suggestive evidence that male chimpanzees give loud "pant-hoot" calls in order to attract females to fruit trees. Sekulic (1981), however, regards *Alouatta seniculus* roars as a direct form of intrasexual competition, as in red deer (Clutton-Brock *et al.*, 1983), whereas Byrne (1982) contends that *Papio papio* calls may warn predators of the ill-advisability of nocturnal attack. *Indri* song, moreover, appears to function in several disparate areas of the animal's normal activities (see summary below).

To demonstrate territorial aspects of primate loud calls properly, it is necessary to make experimental interventions such as playback or suppression, preferably both. Playback experiments have been widely used recently (Waser, 1975; Chivers and MacKinnon, 1977; Robinson, 1979; Kinzey and Robinson, 1983; Mitani 1985; Raemakers and Raemakers, 1985) and these have amply demonstrated the sensitivity of the animals, the problems in obtaining adequate comparable responses, and the difficulty of interpreting the impact of the event on the animals' *normal* behavior (see Byrne, 1982). Both dispersion (Waser, 1975) and aggregation (Robinson, 1981) have followed well-designed playback trials, and these results probably reflect functional properties of the normal calls. One major difficulty is well illustrated in Mitani's (1985) admirably full playback trials with *Hylobates muelleri.* Because the most likely function of duetting in this species is to *deter* territory intruders, the expected behavioral responses to playbacks may be negative or ambiguous. Too many playback experiments have shown dramatic changes in behavior only when extreme social disturbances are simulated, such as experimental calls from territory centers. These simulate conditions the natural calls are presumably functioning to prevent.

An alternative technique is experimental suppression and animal removal, which has been attempted only for two species of primates, both prosimians: *Lepilemur mustelinus* (Charles-Dominique and Hladik, 1971) and *Phaner furcifer* (Charles-Dominique and Petter, 1980). In both species, the results of caging a male in his territory, and subsequently removing him from the territory altogether, demonstrated clearly how the position of the calling male relative to conspecifics and the male's physical presence (cf. playbacks) were *both* implicated in maintaining territorial integrity. These pioneering experiments, furthermore, showed how territorial encroachment and takeover proceeded while permitting the researchers to strictly define and measure the experimental intervention. Similar studies in the hylobatids, *Callicebus* spp., and *Indri* would be extremely useful.

Studies of the natural history of primate loud vocalizations without employing experimental techniques, however, involve as many explanations as there are forms of natural variation in vocal behavior. Studies of siamang and lar gibbons, for example, have identified calling frequencies which correlate positively with fruit availability and with the mating season and other social upheavals and are decreased by "tragedies and gross disturbances" (Chivers and Raemakers, 1980). Whitten (1982) determined an interesting positive relationship between male calling frequency and subsequent travel length to fruit trees.[5]

In the present study, evidence has been presented to suggest that *Indri* song functions in a variety of ways. This evidence can be summarized as follows.

(1) The song's physical structure is such that the adult male (song initiation and unique calls), adult female (continuous singing), and other individuals (varying, incomplete contributions) supply long-range, putative information on age and sex and, perhaps, breeding condition. Further group composition information is provided by the association between group size and song duration.

(2) Singing activity increased in midsummer by a factor of 6, when the corresponding increases in activity period and ranging distance were, respectively, 51–59 and 70–95% (Pollock, 1975a,b). This seasonal peak implies a reproductive function to the song, as breeding behavior occurs at this time.

(3) Although study groups responded with songs more frequently to groups in the near-distance than further away, neighbors' songs were not always answered. This suggests the characteristics of the surrounding population, in addition to the behavior of the nearest groups, are important to each group. Responses to groups up to 1200 m from a territory center were very common, placing each *Indri* group in direct vocal contact with at least 20 others in areas of high *Indri* density.

Groups in some parts of the forest have a singing rate that is consistently higher than that of other groups and this variation is not clearly related to group density. It may characterize regions of territorial dispute.

(4) Singing plays a central role in encounters between groups when males confront each other or other groups at territory borders. The synchronization of calls by group members in their song may achieve the most significance on these occasions (and when individuals "lose" other group members in the forest), when they can be widely separated in space.

Most singing interactions between groups occur early in the day's activities, but no impact of song on preceding or succeeding ranging behavior could be determined.

(5) Songs emitted by single individuals possessed the adult male structure only, and in the one established case such an individual was determined to be a male ranging alone without a territory. Group formation may, therefore, occur as a result of male migration and the location of a group-living young female.

An integrated model of the intergroup communicative processes exhibited by *Indri* is presented in the following paragraphs. Although this model

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[5] Such a relationship might be satisfactorily explained should the territorial security obtained by calling allow the individual to forage further from disputed boundaries.

cannot be supported by conclusive evidence at present, its heuristic value seems sufficient to warrant its presentation here as a basis for further study and discussion.

(1) The morning songs of *Indri* function, evolutionarily speaking, (a) to announce the occupation of an approximate region in the forest to *distant* groups or individuals (this may be particularly true for "single" calls) and (b) to advertise the present location within an already defined area (defined possibly by repeated group confrontation) to neighboring groups (especially clustered or ABA-type call groups).

The wide frequency spread of the energy in *Indri* song does not apparently conform as a straightforward adaptation to long-distance propagation of the call as a single message: "call or no-call." This is, however, an extremely complex subject (Marten *et al.*, 1977), and it may be that the *Indri* vocal strategy is one of competing high attenuation rates with high source-sound levels (Waser and Waser, 1977).

(2) For any individual animals that may be nomadic, songs from parts of the forest over a period of time may, in addition, reflect the population density within that region (and hence the potential for mate location and/or territory formation). The actual regions occupied may be communicated to these individuals by scent-marking in the territory (Pollock, 1975b). Characteristics of some groups' songs may provide information on the reproductive state of their constituents. Both these features may have significance only at certain times of the year. Such a functional characteristic may exist as a consequence of *Indri* singing patterns rather than a cause.

(3) A single song is therefore purported to transmit different information to different individuals or groups. As suggested above, the actual lines demarcating a territorial boundary may be established over a long period of time—probably several years—by group confrontations that are lengthy, intense, and perhaps traumatic for the individuals involved. This is important, for it probably facilitates memory of the exact location for both groups. The integrity of a territory for a single group, in this case, would be dependent on the duration of its occupation and maintenance.

(4) Thus, neighboring groups probably maintain a distinct familiarity with each other mediated mostly by vocal interaction and also by occasional visual and/or physical encounters. The most likely role of scent-marking (if this is indeed communication directed outside the group) lies in its signaling properties for conspecifics that have abandoned or lost strict ranging limitations and are, therefore, not involved in intergroup encounters.

(5) The songs additionally function to bring dispersed group members together and as part of the ritual of intergroup border encounters.

(6) Songs are emitted usually in response to some external auditory stimulus, most often the songs of other groups; but apparently "spontaneous" songs suggest a general motivation to sing in the morning, early in the day's

ranging activities. Songs induced by alarms or disturbances might function to alert related individuals should territory reformation be a family affair, as envisaged by Tenaza and Tilson (1977) for *Hylobates klossi.*

Prominent social behavior, such as loud calls, may function differently in different social conditions. If they are important for promoting mate selection and location only at very low *Indri* population densities, functional explanation in field situations where each group can hear the calls of up to 100 others would be confounded. Functional adaptations of loud calls may be obscured or emphasized at different population densities, which might account for the varying functions attributed to gibbon calls in different studies (see Tenaza, 1975). Unitary explanations of function are therefore ill-advised, if not insufficient, in many cases. However, no evidence was obtained in this study to suggest that contagious calling in *Indri* is a two-way communicative interaction because the behavior of study groups after their songs were "replied" to did not differ from their behavior after singing without "reply." Neither did spontaneously emitted songs differ in associated behavior from calls made "in reply."[6] It is, therefore, at present most reasonable to suggest that *Indri* usually sing "for their own purposes" rather than to induce singing in other groups.

Indri and *Hylobates* spp. have converged remarkably in their loud calls and other behavior (Pollock, 1986), which makes it tempting to seek similar functional explanations in both cases. Certain nearby calls induce approach and display in both genera, illustrating strong territorial associations; and their songs likewise can act to effect reaggregation of dispersed individuals. There are, in addition, some details of great similarity. For example, a study on *H. lar* songs reported that "we also tape-recorded a group in Huay Kha Khaeng in which the two males gave codas to the (female) great calls one after the other... they were definitely from the same group, and were presumably father and son..." (Raemakers *et al.,* 1984), recalling very closely the singing pattern in Group P.

Nevertheless, hylobatid duets appear to be much more socially structured than *Indri* duets. In *Hylobates,* the two sexes generally organize their calls so as to call together or separately. In *Indri,* however, integration is only at the level of the whole song; once it has started, males apparently play out their singing roles independently of females. Furthermore, gibbons spend much more time vocalizing than *Indri* (Raemakers *et al.,* 1984), and the calls may not convey information much beyond neighboring territories (Mitani, 1985), unlike *Indri.* It has been suggested, from observational and experimental (playback) data on female-only vocalizations, that the songs of *H. agilis* (Gittins, 1978). *H. lar* (Raemakers and Raemakers, 1985; Raemakers *et al.,* 1984), and *H. muelleri* (Mitani, 1984) function to discipline a potentially

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[6] It is possible that the number of spontaneous songs is actually very small and largely constitutes an artefact of the superior hearing of *Indri* over man.

unstable monogamous relationship between the adult pair. It is unlikely that females call alone in *Indri* and this contingency cannot therefore be easily examined. However, a strict physical dominance of adult female *Indri* over males exists in the course of their normal activities, which may obviate the functional need for such behavior (Pollock, 1979a).

It seems likely that at some point in the evolutionary separation of *Indri* from an ancestral indriid stock, the role of communication by active scent deposition was replaced by vocal exchange. *Indri* engage in scent-marking *behavior* (it is not certain that scent is actually deposited) at relatively low frequencies (Pollock, 1975b) compared to *Propithecus diadema* (personal observations) or *Propithecus verreauxi* (Richard, 1975). Furthermore, both *Phaner furcifer* (Charles-Dominique and Petter, 1980) and *Lepilemur mustelinus* (Charles-Dominique and Hladik, 1971), which emit frequent, contagious calls (especially at territory borders), do not frequently scent-mark, although this behavior is widespread in other nocturnal lemurs. Explanations are needed to account for this switch in channels of communication, which parallels developments in the haplorhine primates.

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