



## The Indris of Anjanaharibe-Sud, Northeastern Madagascar

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*During a short field trip to the Special Reserve of Anjanaharibe-Sud in northeastern Madagascar, data concerning pelage coloration, behavior (especially vocalization), and ecology of indris were collected. Anjanaharibe-Sud is the northernmost locality of indri distribution. In comparison to the better-known indris from the southern part of their distribution, the indris in this region show different pelage coloration. Several types of loud vocalizations are analyzed, based on a small sample of tape recordings. Their song structure is more complicated than previously reported, containing distinct sequences of duetting. Data on behavior and ecology were collected by interviewing guides and local inhabitants. Some information contrasts with reports on the more southern indri populations. The conservation status of indris in Anjanaharibe-Sud and the future of the reserve are outlined.*

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**KEY WORDS:** indri; Madagascar; *Indri indri*; vocalization; duet song.

### INTRODUCTION

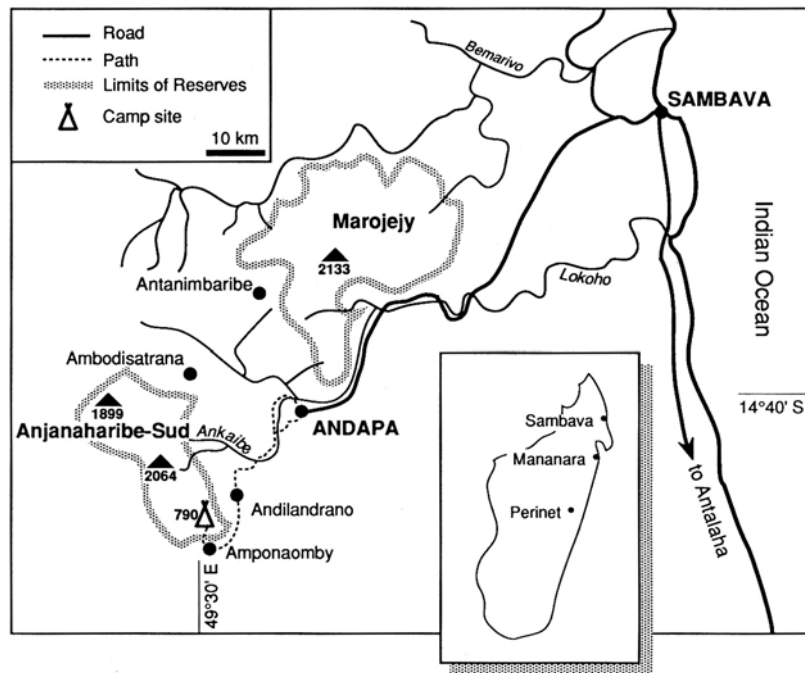
*Indri indri*, the largest extant lemuriform primate of Madagascar, is severely threatened by habitat destruction, and is classified as an endangered species in the latest IUCN Red Data Book (Harcourt and Thornback, 1990). Its present distribution is confined to the eastern rain forest, approximately between the latitudes of Mahanoro and Sambava, ex-

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cluding the Masoala peninsula (Petter *et al.*, 1977; Tattersall, 1982). In the northern part of its distribution, the indri is generally considered to be “at best exceedingly rare” (Tattersall, 1982, p. 91). Indris are not known to occur in the Marojejy Reserve situated northwest of the Andapa Basin (Fig. 1). On the other hand, indris were recently reported to be still present in the “Réserve Spéciale” (RS) of Anjanaharibe-Sud, southeast of the Andapa Basin (Nicoll and Langrand, 1989). This appears to be the northern limit of their distribution.

We report preliminary observations on the indris in Anjanaharibe-Sud. They are of special interest because most previous information on indris was collected in localities in the southern part of their range of distribution, especially in the region of Perinet.



**Fig. 1.** Location of the RS (Special Reserve) Anjanaharibe-Sud and our camp site (schematic map after Nicoll and Langrand, 1989). Inset map: Madagascar.

## MATERIAL AND METHODS

### Data Collection

Three of us (U.T., A.S., and T.M.) visited the southern part of the RS Anjanaharibe-Sud for 6 days (4–9 October 1990) in order to look for indris (camp at about 14°46'S; 49°30'E, altitude 790 m). At that site, we collected data on external appearance (four individuals) and vocalizations, supported by video- and audio-recordings. Additional information was obtained from local guides.

For comparison of pelage coloration, skins of indris from known localities were studied in the British Museum of Natural History in London ( $n = 8$ ) and the Rijksmuseum van Natuurlijke Historie in Leiden ( $n = 9$ ). In addition, photographs of individually distinguishable animals from Pollock (1975b) were analyzed as far as possible ( $n = 7$ ). All but three individuals [two from Pollock (1975b) and one specimen observed by us in Anjanaharibe-Sud] were probably adult; the others appeared to be subadult. Seven characters of the pelage coloration were evaluated, of which five are considered in this paper (Table I).

For vocal comparison, several tape-recordings of indri vocalizations collected in August 1968 at Perinet were made available by Professor R. D. Martin. Additional vocalizations contained on several television films were also included in the comparison (Attenborough and Blanchard, 1969; Attenborough and Parsons, 1980; Herzog and Wothe, 1989; Salisbury *et al.*, 1988). Finally, various gibbon songs tape-recorded by one of us (T.G.) were available for comparison. The song excerpt used for a sonagram was tape-recorded at the Metro Zoo in Miami (U.S.A.) on 31 September 1988.

**Table I.** Selected Fur Coloration Characteristics and Corresponding Character Code Used for Analysis.

Character	Character state		
	Code 0	Code 0.5	Code 1
Light face ring	Absent or incomplete	Full, but narrow	Full, broad
Light occipital patch	Absent	Gray	White
Light lateral collar	Absent	Distinct, restricted to lateral throat	Distinct, extends up to behind ears
Outer side of forearm	Black, blackish	Dark gray	Grayish or whitish
Outer side of hind limb	Black, blackish	Dark gray	Grayish or whitish

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On some tape-recordings, several indris are vocalizing together. In order to identify the notes uttered by each individual, we relied on characteristics that we were able to recognize on the tape-recordings or on the sonagrams (such as similarity of note shapes, recurrent patterns of note combinations, intensity of the various song contributions, or overlapping contributions), since we were unable to film or to observe the animals directly while they were singing. Although we believe that we correctly assigned most of the notes to the singing individuals, this method is not completely reliable.

Coordinates for Malagasy localities other than Anjanaharibe-Sud mentioned in this article were extracted from the Official Standard Names Gazetteer no. 2 (United States Board on Geographic Names, 1955).

Spearman Rank Correlation Coefficients were computed using the StatView II statistics software.

### Sonographic Devices

All tape-recorded indri vocalizations were digitized on a Macintosh II computer using the SoundRecorder device (Farallon). The sampling rate is defined as “the number of intervals per second used to capture a sound when it is digitized” (Schmidt *et al.*, 1989, p. 222). Unless otherwise stated, all sounds were sampled at a 5-kHz sampling rate, thus removing frequencies above 2.5 kHz (Schmidt *et al.*, 1989). Sonagrams of all indri vocalizations were generated with the program SoundEdit, Version 2.0.1 (Farallon). The sonagrams were then copied to an image-editing program (Image, NIH, version 1.14u), with which background noise and echo effects were removed.

### Terms and Definitions

A *note* is a single, continuous sound of any distinct frequency modulation, produced by either an inhaled or an exhaled breath. A *phrase* is a larger and looser collection of notes identifying a single vocal activity, whereas *sequences* refer to vocal and nonvocal behaviors which are more closely related to each other than to preceding and succeeding behaviors and which, when taken together, form a single theme. These definitions were developed by Haimoff (1984) for the study of gibbon vocalizations.

Following the definition of Thorpe (1961, p. 15) a *song* is “a series of notes, generally of more than one type, uttered in succession and so related to form a recognizable sequence or pattern in time.” A *duet* is defined here as the joint vocalization of two individuals, coordinated in time and/or in selection of distinct note-types (Wickler, 1974).

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## RESULTS

### Population

To judge from the number of loud indri songs we heard, the population density in this region appears to be fairly high. However, it is quite difficult to find and observe the animals. The terrain is very hilly, with steep valleys. Each indri group sings only a few times a day, and even if the observer is very close to the group, the animals may still be well hidden in the canopy at a height of about 20-30 m. We saw a single individual on one day, and a group of 3 animals on the following day, several hundred meters away from the first sighting. According to our guides, the group size is usually two or three individuals; the largest group ever seen by a guide consisted of six animals.

The indris, called "Babakoto" by the local people, are protected in this region by a taboo (*fady*), and are therefore not hunted by the members of the local Tsimihety tribe. They believe that, in early times, indris gave them medicine against injuries caused by fights against invaders with iron weapons.

### Pelage and external characters

Our guides had not observed any obvious variability in the fur pattern of the indris in this region. However, they reported a certain degree of sexual dimorphism and an age change in coloration. The following descriptions are based mainly on the 4 individuals we observed, but are in full accordance with reports from our guides. There is a constant pattern of coloration (Figs. 2 and 3a): The indris are black with a white face ring, white fur on the sides of the abdomen and a white pygal triangle on the back, extending caudally to the gluteal region, including the vestigial tail, and the heels are white to yellowish. The eyes are yellow.

Figure 4 shows the coloration pattern and the variation of five easily recognizable characters (Table I) along a geographical gradient from north to south. The figure uses information on 28 indris from known localities. These include museum specimens, our sightings of indris in Anjanaharibe-Sud, and photographs in Pollock (1975b).

In the north, indris usually have a light face ring, but no light occipital patch and no laterally extending light collar. The outer sides of the lower arm and the leg are black. In indris from the southern region, the face is usually black or sometimes has pale patches over the eyebrows or on the cheeks, with only one specimen in our sample showing a white face ring (Pollock, 1975b, plate 6.4; Freeman, 1978, p. 28, photograph by Pollock).

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**Fig. 2.** Indri in its natural habitat at Anjanaharibe-Sud.

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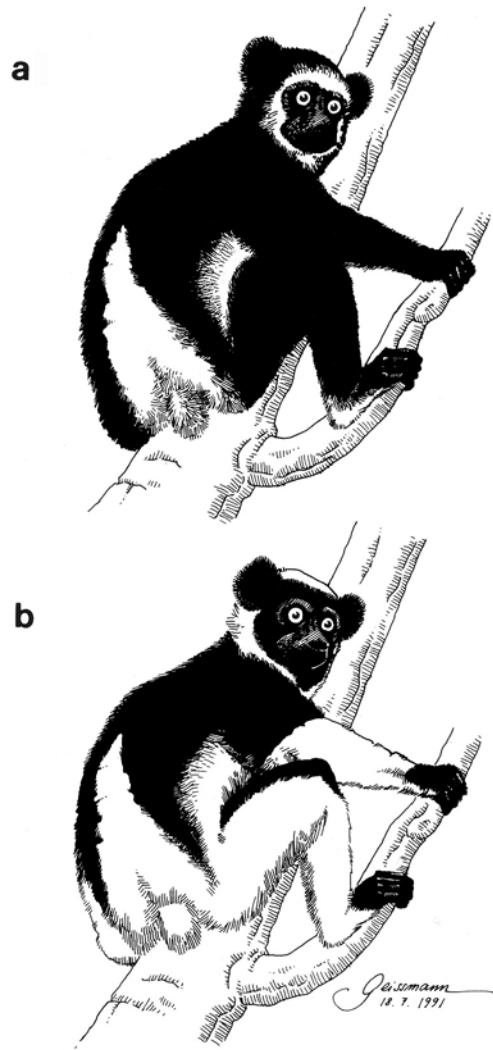
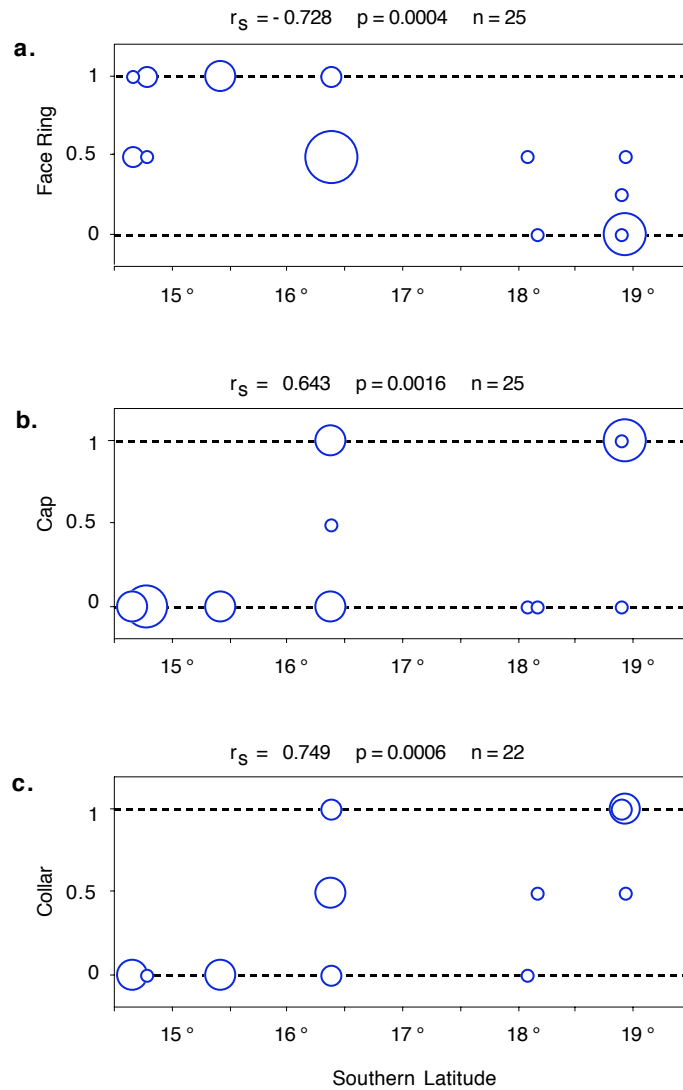


Fig. 3. Indris from Anjanaharibe-Sud (a) and Perinet (b).

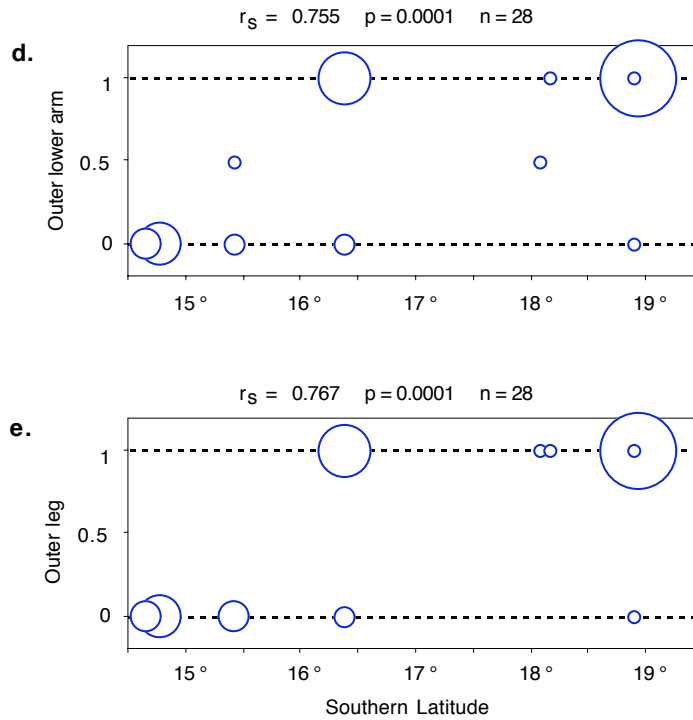
In addition, southern indris exhibit pale or white markings of considerable but variable extent which are usually absent in northern indris: There is a patch on the back of the head (occipital patch) and a lateral light collar extending up behind the ears in most southern individuals. The outer sides of the forearm and hindlimb are grayish or whitish (Fig. 3b).

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**Fig. 4.** Frequency distribution of selected characters of pelage coloration (each encoded from 0 to 1 on the vertical axis) along a gradient from north to south (horizontal axis). (a) Face ring; (b) occipital patch; (c) lateral collar; (d) outer side of forearm; (e) outer side of hindlimb. The diameter of the circles is proportional to the number of specimens with the same character code. The key to the character code is presented in Table I. Above each graph, the Spearman Rank correlation coefficient ( $r_s$ ) corrected for ties and the error probability ( $p$ ) is shown.





**Fig. 4.** Continued.

A mixed pattern occurs at the latitude of Mananara (16°23'S, 49°44'E;  $n = 7$ ): All individuals have a face ring, albeit narrow in most of them. The light occipital patch is present in four individuals (white in three individuals, gray in one of them). Most of the individuals from Mananara have grayish outer forearms ( $n = 5$ ) and outer hindlimbs ( $n = 5$ ).

### Vocalizations

#### *Circadian Distribution of Songs*

Because they are difficult to spot, the very loud territorial vocalizations (songs) of the indris are frequently the only sign of their presence. Our main aim was to observe them, and the songs helped us to locate them.

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On the mornings of 5 to 7 October, the first morning songs occurred at 0808, 0847, and 0916, respectively. On the first day, we heard the second song at 0815, but we were not sure whether it was produced by the same group or not. A different group was heard at 0848, and 4 min later a third group began to sing. A single individual vocalized at 0903. A particularly intense period of singing occurred from about 1040 to 1100. Standing on a hill, we heard many groups (song cluster). On the second day, we paid special attention to the first group we heard (0847) because it was very close. They vocalized again at 0954, but they uttered "honk" calls instead of songs. The honks were probably a warning signal elicited by our guides, who found the indris at the same time. After 0954 we heard other groups of indris calling from some distance away for several minutes. At about 1100, we again heard songs of several groups, but the group we were observing did not join in, perhaps because of our presence. After 1130 we heard no further calls.

At the time we visited the reserve indri songs were only heard in the morning between 0800 and 1130. Our guides told us that the number of songs depends, to some degree, on the weather; the indris sing more frequently when rain is expected. During the year, the daily frequency distribution of songs appears to change: According to our guides, indris also sing from midnight to morning in April.

#### *Classes of Vocalizations*

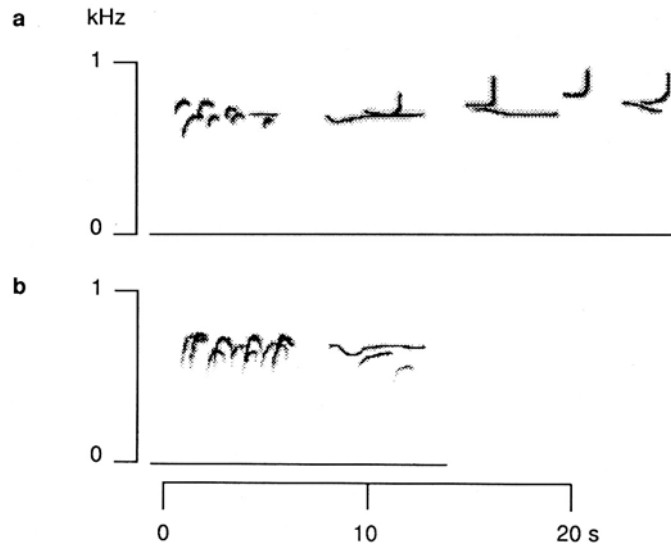
The three different classes of loud indri calls recorded at Anjanaharibe-Sud are briefly described as follows:

*Waa Notes.* This class of vocalization appears in both of the two initial stages of songs tape-recorded at Anjanaharibe-Sud. Waa notes are relatively short, each beginning with a steep rise in frequency, which declines slightly towards the end of the note (Fig. 5a, first half of sonagram). Their fundamental frequency range is about 0.5–0.9 kHz.

Three instances of similar notes were also found among the tape-recordings from Perinet, each occurring at the very beginning of a song (Fig. 5b, first half of sonagram). Waa notes were, on all tape-recordings in which they occurred, uttered by two or more animals as a chorus, here termed a waa sequence. Each waa sequence lasted several seconds and occurred only once, at the beginning of a song. Apparently, no sonagrams of this vocalization have been published previously.

Waa notes were first described by Petter (1962, p. 109) as barks which initiate the song: "aboiements très forts, émis par tous les Indri en même temps, 'ouai-ouai-ouai-ouai'..." Similar descriptions have also been pro-

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**Fig. 5.** Sonagrams showing the transition from the waa sequence to the long note sequence during the initial stages of an indri song. (a) Anjanaharibe-Sud; (b) Perinet.

vided by Petter and Charles-Dominique (1979, p. 278), Petter and Peyri ras (1974, p. 42), Petter *et al.* (1977, p. 402), and Pollock (1975a, p. 305: “loud barking ‘roar’”). According to these authors, this same type of vocalization is also uttered outside of the song context by animals disturbed by aerial predators (Petter and Charles-Dominique, 1979, p. 282; Petter *et al.*, 1977, p. 405; Pollock, 1975a, p. 305).

*The Song Proper.* The notes produced during the song proper, i.e., during the main part of the song following the waa sequence, are highly variable. At Anjanaharibe-Sud, we tape-recorded three duet songs (including one which began as a trio) and a short excerpt of a solo song. Based on this limited sample and on several songs tape-recorded at Perinet, we were unable to differentiate between completely exclusive note classes within the song proper. Although we found many different types of notes following the waa sequence, all types appeared to be linked with each other by notes of intermediate form.

Indri songs usually lasted several minutes. The shortest song on our tapes had a duration of 54 sec, the longest was at least 2 min 47 sec (an initial part of unknown duration was missing from the tape-recording).

The order in which the different note types occurred was also found to be highly variable. However, a general pattern was recognizable, even from

our small sample (and was confirmed by analyzing the comparative sample of songs from Perinet):

*Long Note Sequence:* Especially long notes (up to a duration of 5 sec) were preferentially used at the beginning of the songs, just after the waa sequence described above. These long notes tended to be less variable in frequency (range, 0.6–1.1 kHz) than notes uttered later in the song, which were more modulated. We had the impression that long notes were not an exclusive note class but could gradually develop into more modulated shorter notes. In one solo song from Perinet, long note sequences also reappeared in later stages of the song. The sonagrams in Fig. 5 show the transition from the waa sequence to the long note sequence in two examples: one from Anjanaharibe-Sud and one from Perinet.

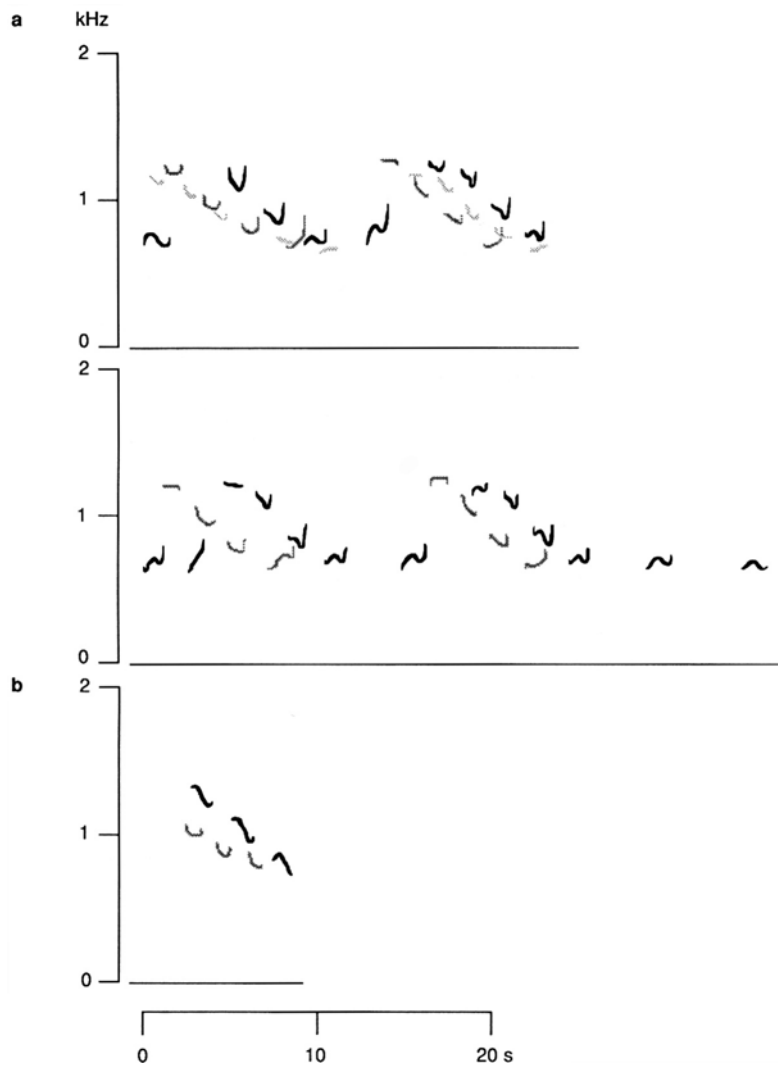
Pollock's (1986, p. 232) "Type I calls" have been described as "long, low calls" of about 0.75 kHz with little frequency modulation, emitted only by the adult males. Possibly, Pollock's Type I call represents the characteristic song element of the long note sequence described above.

*Descending Phrase Sequence:* After the long note sequence, a wailing phrase becomes especially prominent in the indri song. This phrase is here termed a descending phrase. These phrases usually begin with a very high note, followed by one to four notes of progressively lower starting frequency. Thus, descending phrases cover a wide range in their fundamental frequency (0.6–1.7 kHz).

Frequently, two or more indris coordinate the timing of their descending phrases to achieve a stable duet pattern. These vocal exchanges usually consist of two (or more) descending phrases started with an interval of a few seconds. Figure 6a shows all descending phrases produced during an indri song tape-recorded at Anjanaharibe-Sud. The first two phrases are produced by a trio of animals. The following two descending phrases are duets. This song was probably produced by the group described above, consisting of an adult pair with a (probably subadult) younger animal. Duets similar to those described above were also found on the tape-recordings from Perinet (Fig. 6b). In order to enhance the clarity of the sonagrams in Fig. 6, notes of different individuals are distinguished by different shades of gray and black.

In tonal quality, descending phrases particularly resemble the typical female contribution (great call) to the song of gibbons (Hylobatidae). For instance, some notes, produced during a typical indri descending phrase, are almost identical to those of the great call of the white-handed gibbon (*Hylobates lar*). Figure 6 illustrates two notes uttered in succession by each species. In contrast to other sonagrams presented in this paper, the vocalizations in Fig. 7 were digitized at a 22-kHz sampling rate, and all harmonics up to 11 kHz are shown. Note the similarity between the two examples

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**Fig. 6.** Sonograms of descending phrases. Notes of different individuals are indicated by different shades of gray and black. (a) Continuous sonogram of all four descending phrases produced during an indri song at Anjanaharibe-Sud. The first two phrases are produced as a trio, i.e., by three animals; the following two descending phrases are duets. (b) Descending phrase produced as a duet by two animals at Perinet.

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in features such as pureness in tone (i.e., the sound energy is concentrated into narrow frequency bandwidths), fundamental frequency range (restricted between 0.5 and 1.4 kHz), frequency modulation, note duration, interval duration, etc.

The division of the indri song into sequences of waa notes, long notes, and descending phrases describes only a general trend. It is possible that not all indri songs follow this pattern. After the long note sequence, vocalizations other than descending phrases occurred in most of the indri songs analyzed here.

*Honk Notes.* We tape-recorded this type of vocalization in one instance only: On the morning of 6 October, the first song we heard (0847) appeared to be sung very close to us. While we were making a tape-recording of the song, our guides went into the forest to find the singing indri group. Soon after the end of the song, the guides encountered the group described above, which consisted of an adult pair and one probably subadult animal. Apparently as a reaction to the presence of humans, the indris began to utter rhythmic, rapid series of uniform and very short (less

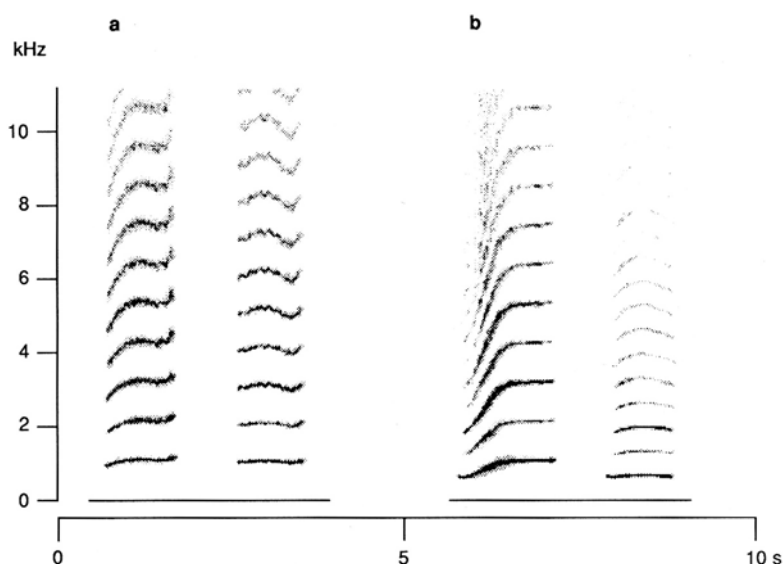
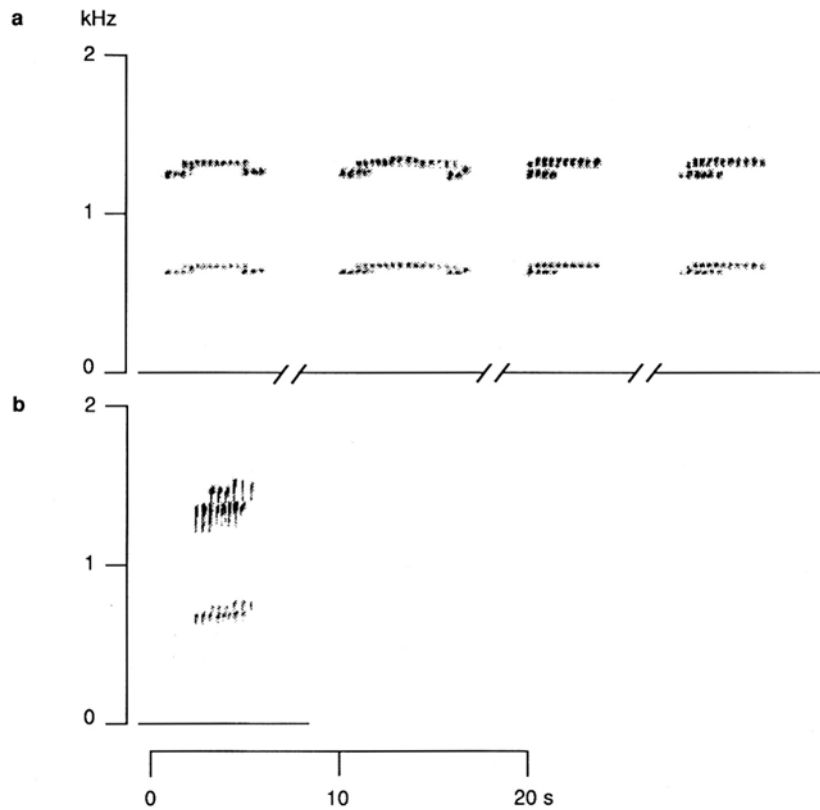


Fig. 7. (a) Two successive notes from a descending phrase, produced during an indri solo song, Perinet. (b) Two successive notes out of the first half of a great call, produced by a female white-handed gibbon (*Hylobates lar*) during a duet song (Metro Zoo, Miami). In contrast to other sonagrams presented in this paper, these vocalizations were digitized at a 22-kHz sampling rate, and all harmonics up to 11 kHz are shown. Note the basic similarity between the two examples.

than 0.5-sec) notes: the honk calls. Eight series of these calls were produced by the group (and tape-recorded by us) within a short time span (2 min 5 sec), although the first series of notes was not completely captured on tape. The average duration of the series was  $5.0 \pm 1.0$  sec ( $r = 3.1\text{--}6.6$  sec,  $n = 7$ ). The series consisted of about  $12 \pm 3$  notes on average ( $r = 8\text{--}17$  notes,  $n = 7$ ). Here the notes uttered by two animals in synchrony were counted only once. The intervals between the series (time lapse between the end of a series and the beginning of the next one) had an average duration of  $12.7 \pm 5.3$  sec ( $r = 6.7\text{--}20.0$  sec,  $n = 7$ ). Like the vocalizations produced during the songs, these calls were also confined to very narrow fundamental



**Fig. 8.** Sonograms of series of rhythmic honk notes. (a) Four series uttered in succession by two indris at Anjanaharibe Sud. Intervals between the series have been shortened for this sonogram. (b) One series uttered by two indris at Perinet. Note that, in each series, two animals vocalize together with different frequencies in a duet-like structure. In this sonogram, the first harmonic (1.3–1.4 kHz) is also shown, because it appears to be of somewhat stronger intensity than the fundamental frequency (650–700 Hz).

frequency bands with many harmonics. In contrast to all other loud indri vocalizations we analyzed, the fundamental frequency of honk calls ( $\approx 0.6$ – $0.7$  kHz) appeared to be of somewhat weaker intensity than the first harmonic ( $1.2$ – $1.4$  kHz). Therefore, we also show the first harmonics on the sonagrams of these calls (see Fig. 8).

The very loud honk notes were uttered by at least two animals of the group, but the identity of the individuals is unknown. The two voices could easily be distinguished because they differed in their frequency: One animal vocalized with a fundamental frequency of about  $0.6$  kHz, the other with a frequency of about  $0.7$  kHz. At the end of some series of honk notes, a few barely recognizable notes of a third animal possibly occurred, but they were too faint to show up on the sonagram.

Interestingly, the two animals vocalized together in a duet-like structure: The first animal would cease to vocalize soon after the second animal joined in but, in four of the seven series (ignoring the incompletely recorded first series) began to vocalize again a few seconds later, shortly before or soon after the end of the partner's uninterrupted series of notes (Fig. 8a). This resulted in minimal overlap between the two animals' vocalizations.

Six of the seven series were initiated by the individual with the deeper voice. In the fourth series, both animals appeared to begin at the same time. After a few notes uttered in near synchrony ( $3.3 \pm 1.4$  notes on average; range =  $1$ – $5$  notes;  $n = 7$ ), the deeper voice stopped, while the higher voice continued as a solo for several notes ( $6.4 \pm 2.0$  notes on average;  $r = 4$ – $10$  notes;  $n = 7$ ). In four of seven series, the deeper voice resumed calling after a few seconds ( $3.1 \pm 0.9$  sec;  $r = 2.1$ – $4.3$  sec;  $n = 4$ ), thus producing a short coda, invariably containing three notes, which concluded the series.

We continued to observe the group for more than an hour after they had stopped giving honk calls, but no further vocalizations were produced. When several other groups began to produce songs around 1100, the group under observation repeatedly appeared to listen to the songs but did not join in, possibly because of our presence.

We found similar vocalizations on two tape-recordings from Perinet. In one of them, a single animal produced a series of honk notes. In the second tape-recording, two animals produced several series of honk notes (Fig. 8b). Again, the two animals uttered their notes together in a duet-like structure, and honk calls were usually started by the individual with the deeper voice. After a few seconds, the second animal would join in. Both animals ended each series of honk notes at about the same time, and both produced most their notes in synchrony, unlike the example from Anjana-

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ribe-Sud described above. The honk calls of the Perinet pair covered a broader frequency spectrum than those from Anjanaharibe-Sud.

Honk calls are probably not functionally related to the more commonly known indri songs. They are probably identical to the calls previously described as very loud calls, like blasts of a horn, by Petter (1962). Similar descriptions have also been provided by Petter and Charles-Dominique (1979, p. 282), Petter and Peyri ras (1974, p. 42), Petter *et al.* (1977, p. 405), and Pollock (1975a, p. 305: "exhaled 'hoot'"). According to these authors, this type of vocalization is usually uttered by isolated animals or animals which have been heavily disturbed by ground predators or observers.

Sonagrams of a series of honk calls uttered by a single animal have been published by Petter and Charles-Dominique (1979, p. 281) and Petter *et al.* (1977, p. 401). According to Petter *et al.* (1977, p. 405), this type of vocalization (even when played back from a tape-recorder) is frequently responded to by another individual with identical calls. According to Pollock (1975 a), this vocalization is only uttered by the adult male and occasionally by his oldest male offspring.

### Behavior and Ecology

The following information was provided by our guides:

One copulation was observed, but at an unknown date. The indris appear to hang under a branch with expanded legs, and to copulate in a ventro-ventral position.

The infants are born from December onwards, but duration of the birth period is not known. Twins have not been observed. During the first 3–4 weeks, the infants are carried ventrally in the inguinal and lateral abdominal region of the mother, between the body and a leg ("ceinture"). Later, they are carried on the back ("sac   dos"). During the period with newborn infants, indris sometimes climb down the trees to a height of about 3 m in order to threaten people which disturb them.

The diet consists of fruits and buds. They mainly consume ripe fruits of *Vongomena* (*Symphonia* sp., Clusiaceae), *Vahamivohotra* (sp. indet.), *Vongo* (*Symphonia cluso ides*, Clusiaceae), leaves of *Tavolo* (*Ravensara madagascariensis*, Lauraceae), and buds of *Tafonana* (*Mespilodaphne faucheri*, Lauraceae). One guide reported that an indri once caught a "moucheron" (a mosquito, but here possibly referring to a horsefly) and brought it to its mouth. It is not known whether the insect was eaten or not.

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In November and December indris move down in the canopy and occasionally come down to the ground in order to avoid contact with the “mouchérons”, which are very abundant at this time. On the ground, landings between jumps are on all four limbs.

## DISCUSSION

### Coloration and Taxonomy

The best known indri populations are those near Perinet (Forêt de Analamazoatra), Maromiza (Forêt de Vohidrazana) and Fierenana (Forêt de Sahamanga) which have been studied extensively in the field by Pollock (1975a,b, 1977, 1979, 1986). Published photographs and video-films from these southern localities (Attenborough and Parsons, 1980; Attenborough and Blanchard, 1969; Herzog and Wothe, 1989; Paulian, 1981; Pollock, 1975a,b, 1977, 1986) show that the indris there differ markedly in their coloration from the indris described here (Figs. 3a and 3b).

However, based on series of wild-shot animals housed in several zoological collections, the pelage of indris has previously been reported to be much more variable (Milne-Edwards and Grandidier, 1875a,b). In their beautiful oeuvre, Milne-Edwards and Grandidier (1875b: plates 11 and 12) figured two indris from the forest of Alamazoatra. The first plate shows a very dark animal, the same black specimen previously portrayed in Sonnerat (1782: plate 88). It is Sonnerat's plate which apparently served as basis for Gmelin's (1788) first description of *Lemur indri* (cited after Tattersall, 1982, p. 89). The second specimen more closely resembles the indris known from Perinet today. Based on their study of museum specimens, Milne-Edwards and Grandidier (1875a) reported that light and black individuals had occurred together in the same troop in the forest of Alamazoatra. Unfortunately, we were not able to find Alamazoatra on our maps, and the name does not figure in the Official Standard Names Gazetteer of Madagascar (United States Board on Geographic Names, 1955). The name resembles Analamazoatra, a forest near Perinet, but only light indris have so far been described and figured from the latter locality (e.g. Pollock, 1975b, 1986).

An almost black indri has also been figured in the following publications: MacKinnon *et al.* (1986; photograph by Petter), Petter and Peyriéras (1974), and Schultz (1972: photograph by Petter). These photographs probably all represent the same individual kept in captivity during >1 year at Ivoloina (Petter *et al.*, 1977). Ivoloina (15°34'S; 49°38'E) is situated in the northern part of the indris' distribution range, not very far from Anjanaharibe-Sud (at about 14°46'S; 49°30'E).

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It is generally assumed that indri "pelage coloration and pattern are highly variable, but this variation is not consistent geographically, except to the extent that there is – perhaps – a tendency on the average toward a slightly lighter coloration in the south of the range" (Tattersall, 1982, p. 90; see also Buettner-Janusch and Tattersall, 1985; Petter *et al.*, 1977). This vague interpretation is not supported by our data. In contrast, northern and southern indris examined by us exhibited completely different coloration patterns, suggesting two clearly distinguishable populations: a dark one from the northernmost distribution range, and a lighter one from the more southern region. Specimens from intermediate localities may eventually be found to exhibit more variability in color pattern, although this is not yet certain. Coloration characters appear to change geographically in a more differentiated way than the term "tendency" would imply. Our results suggest that characters do not all change at the same latitude, and not in a gradual way. The most drastical change of coloration between the two populations may, however, occur in the region of Mananara.

Observations published by Schwarz (1931) appear to contradict our data in two respects: (1) He mentions that specimens from the east and north of the Bay of Antongil (north of Mananara) have a tendency to show gray forelimbs and hindlimbs, whereas south of the Bay of Antongil, they usually have dark brown limbs. In contrast, the specimens from north of Mananara examined by us correspond to the pattern of other northern populations in having dark limbs with virtually no gray (one specimen of nine had some dark gray on the outer side of the forelimbs). (2) In addition, (Schwarz, 1931, p.425) found "hardly any variation in the fifteen specimens collected at Sakana, north of Tamatave, by Prof. Voeltzkow". He reported that this indri population had dark limbs. Although we were unable to locate "Sakana" precisely, our data suggest lighter-colored indris for the region of Tamatave. Because of the contradiction described above, the question of whether the indris comprise only one highly variable taxon or two or more distinct populations cannot be reliably answered at the moment. Our data support the second hypothesis. Current knowledge of variation of indri coloration is greatly limited, due to absence of or inaccuracy in locality records for museum specimens and the inadequate definition of fur characteristics cited previously. We intend to study further museum collections and wild populations of indris.

### Vocalizations

The loud calls or songs of indris are probably the feature which most struck the attention of previous observers. Pollock (1986) discussed several

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possible functions of indri songs, most of which are in some way related to territorial announcement and defense. However, the organization of these loud calls has apparently not been analyzed in much detail. Even the analysis of our very small sample of tape-recordings from Anjanaharibe-Sud and from Perinet revealed song structures which have apparently been incompletely documented in previous accounts.

Only a few sonagrams of indri songs have been published so far (Haimoff, 1986; Petter, 1962; Petter *et al.*, 1977; Petter and Charles-Dominique, 1979; Pollock, 1986). Most of these failed to reveal any structural segments within the song either because they were too short (Petter, 1962; Petter *et al.*, 1977; Petter and Charles-Dominique, 1979) or because the frequency range they covered was too large to reveal any details of the note structure (Pollock, 1986).

The frequency range of the indri song has been variously reported to cover 0.5–2 kHz (Haimoff, 1986), 0.5–4 kHz (Petter and Charles-Dominique, 1979; Petter *et al.*, 1977; Petter and Peyri ras, 1974), and 0.5–6 kHz (Oliver and O'Connor, 1980; Petter *et al.*, 1977; Pollock, 1975a, 1986). These reports are obviously mutually incompatible. The problem probably arose because different authors measured different frequency bands, without explaining what exactly they measured. We found that most energy of the indri song vocalizations is concentrated in the fundamental frequency bands. If only fundamental frequency is taken into consideration, the frequency range covers only about 0.5–1.7 kHz. If harmonics are also to be taken into consideration, it is essential to define which ones. Pollock (1986, p. 232) reported that “pure tones of the call appear with up to four harmonics and may be modulated by as much as 2000 Hz within each call.” However, our analysis revealed that indri (and gibbon) song vocalizations can have up to 10 harmonics below 11 kHz (Fig. 7) and possibly additional harmonics above 11 kHz, which is the highest frequency that can be displayed by our sonagraphing device! The number of harmonics that can be seen on a sonagram probably depends on the quality of the tape-recording and/or the sonagraph device. For this reason we also believe that Pollock’s (1986) statement that indri notes “may be modulated by as much as 2000 Hz” applies only to harmonics. Because the fundamental frequencies during all indri songs analyzed here were situated well within the range of 0.5 to 2 kHz, individual notes cannot possibly include modulations which are larger than the frequency range used by indris. The largest modulation of a fundamental frequency we found within a single indri note amounted to less than 0.5 kHz.

The long and loud vocalizations of indris have repeatedly been termed “songs” (Haimoff, 1986; Oliver and O'Connor, 1980; Pollock, 1975a, 1986). Most indri songs in our sample begin with a sequence of waa calls,

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Followed by a sequence of long notes, and end with a sequence particularly rich in descending phrases. The latter sequence is usually the longest. This relatively complex structure fulfils the conditions contained in our definition of song.

In one relatively long solo song (2 min 47 sec) from Perinet, long note sequences and descending phrase sequences were found to alternate. In addition, each of the three descending phrase sequences began with short descending phrases of two notes; but phrases became progressively longer (up to five notes) during each sequence and reached higher frequencies towards the middle part of each sequence. This observation suggests that some indri songs may follow even more complex rules than those outlined above.

The descending phrase, the most prominent element of the indri song, bears some resemblance to a particular phrase of the gibbon song which is produced by females only: the great call (e.g. Geissmann, 1984, 1993; Haimoff, 1984; Marshall and Marshall, 1976; Marshall and Sugardjito, 1986). Because descending phrases are frequently produced by two animals as to form a duet, we suspect that they are usually produced by mated pairs. Haimoff (1986) published a sonagram of one descending phrase duet, attributing particular notes to the male and others to the female. He did not explain how he deduced this information from tape-recordings. Probably, the duets of descending phrases are produced by mated pairs, but since we did not directly observe the indris while they were calling, we do not know whether this is true.

Although it has previously been suggested that paired indris may utter their songs in the form of a duet (Haimoff, 1986; Pollock, 1986), these reports differ markedly in the description of the indri duets. Pollock (1986, p. 261) described the duet structure of the indri song as follows: "In *Indri*, ... integration is only at the level of the whole song; once it has started, males apparently play out their singing roles independently of females." This finding contrasts with our finding that indris may coordinate the timing of their vocalizations several times during a song, that is, during the descending phrases. On the other hand, the duet structure described in this article is virtually identical to that previously described by Haimoff (1986, p. 55f).

The indri songs we analyzed from Anjanaharibe-Sud are essentially similar to those from Perinet. Although we failed to detect a clear difference between the songs of the northern black indris and those of the paler indris from Perinet, this may also be due to our small sample of tape-recordings.

Another type of vocalization described in this report, the honk call, does not contribute to the indri song. Although honk calls had been men-

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tioned by several authors, a duet-like structure in this vocalization had not been recognized before. In two of our tape-recordings, series of honk notes were uttered as a duet by two animals. The amount of temporal overlap in the vocal contributions of the two animals differed between the tape-recording from Anjanaharibe-Sud and the one from Perinet. In addition, the honk calls from Perinet covered a slightly broader frequency spectrum. Our small sample of tape-recordings is too limited to indicate whether these differences represent individual or populational variation.

### Behavior and Ecology

The report of our guides that in November and December indris move down in the canopy in order to avoid contact with “mouchérons” (= horseflies?) resembles earlier reports: “In the months of October, November, and December, *Indri* were often observed with binoculars while plagued by horseflies and they were seen to make sweeping motions with their hands and feet.” (Petter and Charles-Dominique, 1979, p. 279; Petter *et al.*, 1977, p. 403).

Some of our guides' information conflicts with certain reports from the more southern study areas: Whereas indri births are believed to occur in December or later at Anjanaharibe-Sud, Pollock (1975a) observed attempted copulations in January and February, and he reported that a birth had occurred in May. During our observations in October, indri songs were heard only between 0800 and 1130 in the morning. According to our guides, indris also sing during the night in April. This differs from previous studies carried out in Beanana, 25 km to the west of Rantabe (Petter, 1962; Petter *et al.*, 1977), and in the more southern study sites of Analamazoatra and Vohidrazana (Oliver and O'Connor, 1980; Pollock, 1986), where indris were observed to engage in nocturnal song activities only in late November and December. Beanana is relatively close to Anjanaharibe-Sud (15°44'S, 49°28'E, vs 14°46'S; 49°30'E).

### Threats to Survival and Conservation

Indris generally react very sensitively to disturbance (Petter and Peyri ras, 1974). Furthermore, they are very difficult to keep in captivity: Only one young individual has been kept alive in captivity for more than a year in a Forest Station at Ivoloina (Petter *et al.* 1977). Thus, indris can be protected only in their natural habitat. Although the Tsimihety tribe does not hunt indris, other people who are not aware of the taboo (fady) or who are not native to that region, hunt them. In 1963/1964, a trail was

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constructed through the reserve at Anjanaharibe-Sud in order to connect the provinces Mahajanga and Antsiranana, so the local people believed that access to the reserve was permitted. Penetration into the reserve became much more frequent and people settled within the reserve. There are plans to upgrade the existing trail to a passable road, which will cause a considerable increase in pressure on the reserve. In order to offset this pressure it is necessary to reestablish obvious markers of the reserve's boundaries, to patrol the boundaries, and to inform the local people about the existence of the reserve. For this purpose, adequate personnel, material, and financial support are essential. Research in this virtually unknown reserve should be intensified to emphasize its importance and its status.

### CONCLUSIONS

According to Tattersall (1982, p. 90), indri "pelage coloration and pattern are highly variable, but this variation is not consistent geographically". Our data do not support this view but instead, suggest that geographically distinct populations may exist. Because of the small sample size available to us, additional specimens from precisely known localities need to be studied before any taxonomic conclusions can be drawn.

The organization of indri songs is much more complicated than had been previously assumed. Various sequences can be differentiated within a song, at least one of which (the descending phrase sequence) appears to consist typically of a relatively tightly-coordinated pattern of vocal interaction (duet) between group members. Additional duet patterns may occur in the "honk notes" – loud vocalizations which are not part of the song. Frequency ranges and modulations of indri song vocalizations have not been correctly described in most previous publications. Similarities to the songs of gibbons (*Hylobatidae*) appear to exist both in the frequency structure and in the organization (sequences) of indri songs. Due to the small size of our sample of tape-recordings, possible differences between vocalizations of northern and southern indris cannot be determined reliably.

Intense efforts are needed to save the flora and fauna of the Special Reserve of Anjanaharibe-Sud and to secure this as a natural habitat for the northernmost indri populations.

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