

Intermale Affiliative Behavior in Ringtailed Lemurs  
(*Lemur catta*) at the Beza-Mahafaly Reserve,  
Madagascar

LISA GOULD

Washington University, St. Louis

**ABSTRACT.** Intermale affiliative behavior was studied in three groups of naturally occurring ringtailed lemurs over a one-year period. The adult males in the sample exhibited affiliative behavior with all other males in their social groups; but affiliative behavior between some male-male dyads occurred markedly more often than between others. These dyads are called "preferred partnerships." The formation of preferred partnerships did not appear to be influenced by male dominance rank or age-class. Furthermore, these partnerships were of a short-term nature, and none persisted throughout the entire study period. The following factors may explain the absence of rank or age effects, and the brevity of preferred partnerships: (1) frequent fluctuation in the male dominance hierarchy in each study group; (2) the fact that higher-ranking males may not offer specific benefits to lower-ranking males; and (3) the fact that male dispersal affected the male membership of each group over the 12-month study period. The focal males engaged in significantly more affiliative behavior during the lactation period compared with the other reproductive seasons. Migration partners may offer each other predator protection during the transfer process, and although males that transfer together do not engage in alliance or coalition behavior towards resident males, males transferring in pairs or threesomes are in a better position to spot and defend themselves against attack by resident males. Migration partners also provide social contact for each other while in the process of immigration.

**Key Words:** Ringtailed lemurs; Affiliative behavior; Adult males.

## INTRODUCTION

In primate species characterized by female philopatry and male dispersal, intermale affiliative behavior has, until recently, been reported as infrequent, and most social interactions between adult males have been described as competitive and agonistic in nature (KAUFMANN, 1967; SAAYMAN, 1971; LINDBERG, 1973; SUGIYAMA, 1976; HASEGAWA & HIRAIWA, 1980; RANSOM, 1981; SMUTS, 1985; NOE, 1992; SMUTS & WATANABE, 1990, but see HARDING, 1980). Information from recent studies, however, reveals that intermale affiliative relationships and bonds do exist in some female-bonded multimale-multifemale primate species, and that such relationships are more frequent than had previously been reported (FURUICHI, 1985; HILL, 1994; MITCHELL, 1994; SILK, 1994; HILL & VAN HOOFF, 1994). In this study, I examine intermale affiliative behavior in ringtailed lemurs (*Lemur catta*), a prosimian primate characterized by female philopatry, male dispersal, and female dominance.

HILL and VAN HOOFF (1994) suggest that patterns of intermale affiliative behavior in a species are dependent upon the manner in which females adjust both ecologically and socially. For example, FURUICHI (1985) argued that relationships among male Japanese macaques are influenced by their affiliative relationships with females. Both FURUICHI (1985) and HILL (1994) suggest that females are the preferred affiliative partners of male

Japanese macaques, and both researchers found that when males were unable to affiliate with females, they formed affiliative partnerships with other males.

Factors such as rank and age have been suggested to affect affiliative relationships between males in female-bonded multimale-multifemale primate species. For example, KAUFMANN (1967) found a marked tendency for rhesus macaque males to associate with males of similar rank. MITCHELL (1994) reports that alliances among male South American squirrel monkeys tend to form between individuals of the same age-class and similar rank, while SILK (1994) found that bonnet macaque males tend to interact most often with males of similar age. In seasonally breeding primates, mating, birth, and migration seasons can also affect both affiliative and agonistic relationships between males (see BALDWIN, 1968; JOLLY, 1966, 1967; DRICKAMER & VESSEY, 1973; ROWELL & DIXSON, 1975; SUGIYAMA, 1976; MEIKLE & VESSEY, 1981; CHENEY, 1983a, b; MITCHELL, 1994).

To date, little information exists with respect to patterns of affiliative relationships between males in the primate sub-order Prosimii. Many prosimian species exhibit female dominance (JOLLY, 1966; BUDNITZ & DAINIS, 1975; JOLLY, 1984; TAYLOR, 1986; TAYLOR & SUSSMAN, 1987; RICHARD, 1987; PEREIRA et al., 1990), thus, males in such species might display different kinds of intermale affiliative patterns than those which are found in the largely male-dominant anthropoid primates (see Question 2, below).

The questions and issues that will be addressed in this paper are as follows:

- (1) Do dyadic affiliative relationships exist between *Lemur catta* males?
- (2) If so, are these relationships affected by a male's dominance rank or general age-class? Furthermore, SAUTHER (1992) reported that the highest-ranking males in her study spent more time than lower-ranking males in close proximity to the female core of the group. Such proximity offers males advantages with respect to greater predator protection, and the opportunity to develop affiliative relationships with females, which could potentially lead to enhanced access to estrous females. Do lower-ranking, more peripheral males tend to form affiliative relationships with high-ranking males, which could lead to the advantages outlined above?
- (3) Does the frequency of intermale affiliative behavior change in relation to the strict reproductive seasonality occurring in this species?

I will also describe the affiliative behavior during the immigration process of two focal males that transferred from one study group to another, as well as a relationship that occurred between a severely injured male and another resident male in one of the focal groups.

## METHODS

### STUDY SITE AND FOCAL ANIMALS

*Lemur catta* is found in riverine and xerophytic forests in southern and southwestern Madagascar (JOLLY, 1966; SUSSMAN, 1977). This species lives multimale-multifemale social groups ranging from 5 to 27 individuals, with a sex ratio of approximately 1:1 (JOLLY, 1966, 1972; BUDNITZ & DAINIS, 1975; SUSSMAN, 1977, 1991, 1992; MERTL-MILHOLLEN et al., 1979; SAUTHER & SUSSMAN, 1993). Separate dominance hierarchies are reported for females and males (JOLLY, 1966; BUDNITZ & DAINIS, 1975; SUSSMAN, 1977). *Lemur catta* exhibits marked behavioral seasonality with respect to both the female reproductive cycle (mating, gestation, birth, and lactation), and male migration (JOLLY, 1966; SUSSMAN, 1977, 1991, 1992; JONES, 1983; SAUTHER, 1991).

**Table 1.** Composition of study groups and age-classes of focal males.

	Age-class*
Blue group	
Male <i>B1</i>	Prime
Male <i>B2</i>	Prime
3 adult females	
1 immature	
Green group	
Male <i>G1</i>	Old
Male <i>G2</i>	Old-prime
Male <i>RG3</i>	Young (migrated from Red to Green group during study)
Male <i>RG4</i>	Prime (migrated from Red to Green group during study)
5 adult females	
5 immatures	
Red group	
Male <i>R1</i>	Young-prime
Male <i>R2</i>	Prime
Male <i>R3</i>	Young (migrated to Green group)
Male <i>R4</i>	Prime (migrated to Green group)
Male <i>R5</i>	Prime
Male <i>R6</i>	Old (died 5 months into the study period)
3 adult females	
3 immatures	

\*Young adult: 3–4 yrs; prime-aged adult: 5–9 yrs; old adult: 10 yrs or older.

My study took place between March 1992 and March 1993 at the Beza-Mahafaly Reserve, situated in southwestern Madagascar. The reserve consists of two parcels of forest: one 500 ha parcel of desert-like *Didierea* forest and one 80 ha parcel of gallery forest. This study was conducted in the latter area.

Beza-Mahafaly is the site of a long-term demographic project on *Lemur catta* begun in 1987 (SUSSMAN, 1991). Between 1987 and 1990, all adult animals residing in the eight social groups in the reserve boundaries were captured and fitted with nylon collars, and numbered plastic tags. Demographic, behavioral, and ecological data were collected on the animals in each year between 1987 and 1993 (SUSSMAN, 1991, 1992; SAUTHER, 1991, 1992; NASH, unpubl. data; GOULD, unpubl. data), thus, age-class, tenure in group, and migration status were already known for the adult males in the focal groups at the onset of the study.

This study of intermale affiliative behavior was part of a larger project concerning patterns of affiliative behavior between adult males and all age-classes of conspecifics. Three social groups of *Lemur catta* containing a total of ten adult males were chosen for study. These groups were of varying composition (see Table 1). All three groups had overlapping home ranges, which is consistent with previous studies of the reserve population (SAUTHER & SUSSMAN, 1993). The amount of overlap varied according to variation in seasonal food availability.

#### DATA COLLECTION AND ANALYSIS

Eleven hundred and two hours of focal animal data were collected on the study animals over the 12-month period. The order of focal males sampled was equally rotated and determined at the beginning of each data collection week. Sampling was conducted during the focal groups' active periods which varied according to season and temperature. On-the-

minute focal animal point sampling (ALTMANN, 1974) in the form of one hour sessions was the primary method of data collection. In addition, all-occurrences (ALTMANN, 1974; SLATER, 1978) of agonistic behaviors were recorded, and nearest neighbor data (animals in contact, less than 1, and less than 3m from the focal animal) were collected each 15 min during the one hour session. Unusual or noteworthy events were noted on an ad lib basis. During each focal session of 60 min, the activity in which the focal animal was engaged (from an ethogram of ringtailed lemur behavior adapted from JOLLY, 1966; TAYLOR, 1986; GOULD, 1989) was recorded at one min intervals. If the behavior was affiliative in nature, the identity of the affiliative partner was also recorded. Categories of affiliative behavior were as follows: allogrooming, sitting or resting in contact or near (less than 1m), huddling, or feeding in close proximity (less than 1m).

To determine the true frequency of affiliative behavior, the onset of a bout of an affiliative interaction between a focal animal and another group member was coded differently from the same behavior if it occurred for a duration of more than 1 min. For example, if a focal animal was engaged in a mutual grooming session with a partner for 5 min, the first 1-min interval was recorded as "onset of mutual grooming with partner X," and the remaining four intervals were recorded as "mutual grooming with partner X." Thus, when the data were analyzed, I was able to obtain frequencies of the affiliative interactions of the focal males by tallying the number of the "onsets." For analysis of differences in affiliative behavior between the sample males across particular seasons, the frequency of each focal males' affiliative behaviors was divided by the number of hours of data collected on that animal in the particular season in question, to obtain rates per hour.

For questions concerning measures of association, such as detecting significant differences in dyadic relationships, chi-square goodness-of-fit tests were used. To determine if differences exist between two categories of animals (e.g. high-vs lower-ranking males), and for questions concerning variations in rates of behavior over reproductive seasons, non-parametric analysis of variance tests were used.

#### REPRODUCTIVE SEASONS

Designated dates for reproductive seasons were as follows: post-migration, 1992: March 14, 1992 – May 13, 1992; mating: May 14, 1992 – June 12, 1992; gestation: June 13, 1992 – September 24, 1992; lactation and migration (concurrent): September 25, 1992 – January 25, 1993; post-migration, 1993: January 26, 1993 – March 13, 1993. Migration season was divided into two sub-seasons: early migration (end of September to November 2, 1992) when the two migrating males in the sample began to leave Red group and spend time on their own, occasionally returning to Red group for the night, and migration/integration (November 2 to approximately January 25, 1993) when the two males began spending most of their time, including the night, in Green group.

#### DETERMINATION OF PREFERRED PARTNERSHIPS

Preferred partnerships among the males in the sample were determined by examining the frequency of affiliative interactions between pairs of focal males over each of the reproductive seasons. If two males exhibited a significantly higher frequency of affiliative behaviors *with each other* compared with other males in their group (based on chi-square goodness-of-fit tests), I considered such a relationship a preferred partnership. In cases where the

expected frequency of affiliative interactions in a particular season was too low to use the chi-square test, due to very low frequencies between non-partners, a male-male affiliative dyad was considered a preferred partnership if each of the males exhibited affiliative behavior at least twice as frequently with each other compared with other males in the group.

## RESULTS

All focal males exhibited affiliative behavior with all other males in their groups; however, conspicuous affiliative dyads or “preferred partnerships” occurred among some of the sample males. These preferred partnerships were highly variable according to reproductive season, and no preferred partnership persisted throughout the 12-month study period. In Table 2, I present the preferred partnerships that occurred during the study

**Table 2.** Preferred partnerships.

	Season of partnership	Frequency of affiliative behaviors with males in group (PP = preferred partner)	Length of partnership (weeks)
<b>Green group males</b>			
<i>G1</i>	Migration	With <i>G2</i> = 29 (PP)*** With <i>RG3</i> = 0 With <i>RG4</i> = 2	10
<i>G2</i>	Migration	With <i>G1</i> = 25 (PP)*** With <i>RG3</i> = 3 With <i>RG4</i> = 5	10
<i>RG3</i>	Migration/post-migration	With <i>RG4</i> = 85 (PP)*** With <i>G1</i> = 0 With <i>G2</i> = 4	16
<i>RG4</i>	Migration/post-migration	With <i>RG3</i> = 89 (PP)*** With <i>G1</i> = 1 With <i>G2</i> = 9	16
<b>Red group males</b>			
<i>R1</i>	Gestation	With <i>R2</i> = 10 (PP) With <i>R3</i> = 0 With <i>R4</i> = 2 With <i>R5</i> = 1	21
<i>R2</i>	Gestation	With <i>R1</i> = 17 (PP)*** With <i>R3</i> = 5 With <i>R4</i> = 2 With <i>R5</i> = 3	21
<i>R3</i>	Early migration	With <i>R4</i> = 14 (PP)*** With <i>R1</i> = 9 With <i>R2</i> = 0 With <i>R5</i> = 4	5
<i>R4</i>	Early migration	With <i>R3</i> = 14 (PP)*** With <i>R1</i> = 9 With <i>R2</i> = 0 With <i>R5</i> = 7	5

Significance level for each preferred partnership where it was possible to calculate chi-square goodness-of-fit: \* $p < 0.02$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ . It is important to note that each preferred partnership is reciprocal (e.g. If *G1*'s preferred partner during migration season was *G2*, then *G2* also had to exhibit a preferred partnership with *G1* in order for the partnership to be considered a preferred one). Males *R3* and *R4* migrated from Red to Green group, and from then on were referred to as males *RG3* and *RG4*.

period, the frequency of affiliative behaviors exhibited by each preferred partner compared with other males in the group, the reproductive season or seasons in which the partnership occurred, and the duration of the preferred partnership. Because there were only two males in Blue group, they were not included in Table 1. The males in Green group were considered only after the immigration of the two males from Red group, as there were only two males in this group prior to the immigration period.

#### DOMINANCE RANK AND AGE OF PREFERRED PARTNERS

Dominance structure among the males, and the rank of each male in each group was

**Table 3.** Rank and age of preferred partners.

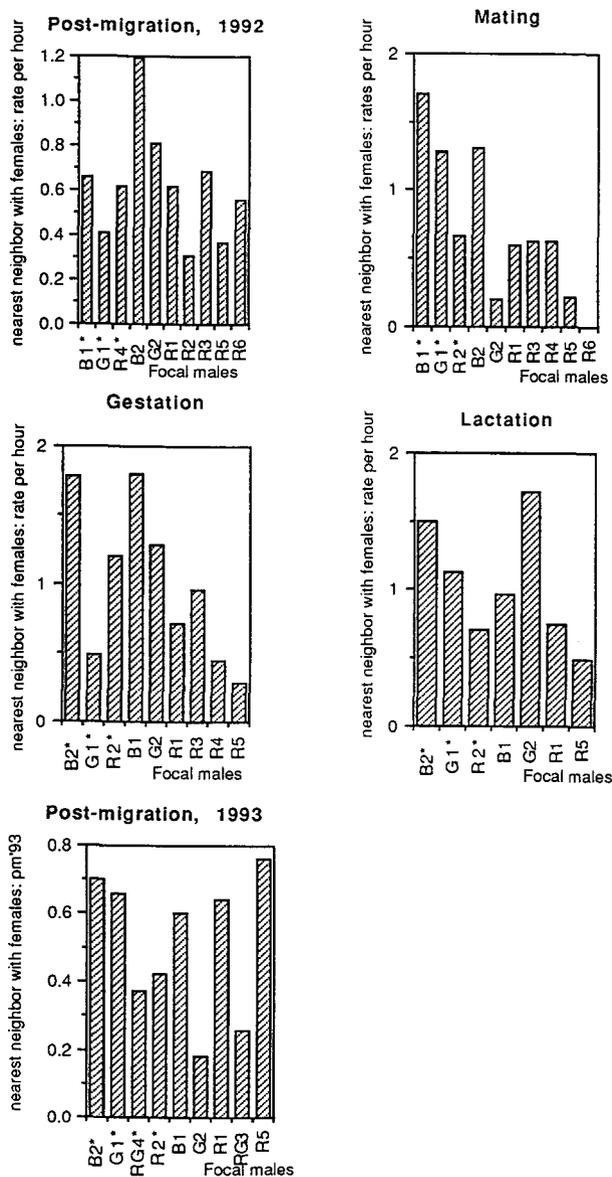
Partners	Rank of each partner	Age-class of each partner
Green group		
<i>G1 &amp; G2</i>	High/middle	Old/prime
<i>RG3 &amp; RG4</i>	Low/middle (upon migration to Green group)	Young adult/prime
Red group		
<i>R1 &amp; R2</i>	Low/high	Young prime/prime
<i>R3 &amp; R4</i>	Low/high (while in Red group)	Same as <i>RG3/RG4</i>
<i>R4 &amp; R5</i>	High/middle	Prime/old prime
<i>R5 &amp; R6*</i>	Middle/low	Old prime/old

\*Affiliative relationship between severely injured male (*R6*) and other resident male (*R5*) from onset of *R6*'s injury until his death two months later.

**Table 4.** Ranks and rank changes of focal males.

Focal male	Rank at onset of study	Rank change and when it occurred
Blue group		
<i>B1</i>	Higher of the 2 males	Lower of the 2 males: September 1992 (6 mos. into study)
<i>B2</i>	Lower of the 2 males	Higher of the 2 males: September 1992
Green group		
<i>G1</i>	Higher of the 2 until migration	Became lower-ranking than <i>one</i> of the new immigrant males ( <i>RG4</i> ) remained higher-ranking than the remaining 2 males (non-transitive dominance relationship)
<i>G2</i>	Lower of the 2 until migration	Remained lower-ranking than <i>G10</i> after migration; however, was consistently higher-ranking than the 2 immigrants
<i>RG3</i>	In Red group at onset	Lowest-ranking male in Green group after migration
<i>RG4</i>	In Red group at onset	Low-ranking male during migration; <i>but</i> was dominant to <i>G1</i> shortly after migration
Red Group		
<i>R1</i>	Low (5/6)	Remained low throughout the study, 3/3 after migration
<i>R2</i>	Middle (3/6)	Rose to 1/6 after mating, remained the highest ranking male in Red group
<i>R3</i>	Low (6/6)	Remained low, migrated to Green group, remained low (see <i>RG3</i> )
<i>R4</i>	High (1/6)	Fell to 2/6 after mating, then migrated to Green group (see <i>RG4</i> )
<i>R5</i>	High (2/6)	Fell to 4/6 after mating period rose to 2/3 after migration
<i>R6</i>	Middle (4/6)	Fell to 6/6 after mating season when severely injured and remained lowest until his death in August 1992

determined by observing the direction of approach/retreat interactions, and the direction of agonistic and submissive signals between males in the group. Males of most of the possible rank combinations and age-classes formed dyadic partnerships. With respect to partnerships and dominance rank, it is important to note that the male dominance hierarchy in all three study groups varied over the 12-month study period, and the majority



**Fig. 1.** The frequency with which high-ranking and low-ranking males were the nearest neighbors to the females in their groups. High-ranking males are noted by an asterisk beside their name. Note the variation in the male dominance hierarchy in each group according to reproductive season.

of the focal males moved from lower to higher rank or vice-versa. The preferred partnerships, the dominance rank of each male in the dyad at the time that the partnership occurred, and the age-class of each male are presented in Table 3. Table 4 illustrates the changes in male dominance rank that occurred during the study period.

Since a number of the partnerships involved males of high rank, and since SAUTHER (1992) found that high-ranking males in her sample at the same site had greater access to the female core of the group, I wanted to examine if a lower-ranking male might benefit from a partnership with a high-ranking male in terms of greater opportunities for proximity to the central female core of the group. I examined the frequency with which high-ranking males were the nearest neighbors to the females in their group, and compared that to the frequency with which lower-ranking males were the nearest neighbors to females (Fig. 1). Higher-ranking males were not the nearest neighbors to adult females significantly more often than lower-ranking males in any season (Mann-Whitney  $U$ -test: post-migration, 1992:  $N1=3$ ,  $N2=7$ ,  $U=9$ , N. S.; mating:  $N1=3$ ,  $N2=7$ ,  $U=19$ , N. S.; gestation:  $N1=3$ ,  $N2=6$ ,  $U=11$ , N. S.; lactation:  $N1=3$ ,  $N2=4$ ,  $U=7$ , N. S.; post-migration, 1993:  $N1=4$ ,  $N2=5$ ,  $U=12$ , N. S.). Lower-ranking males who were *not* partners with high-ranking males exhibited comparable or higher (in some seasons) nearest neighbor rates with females compared with the highest ranking males in their groups. In Red group, for example, low-ranking male *R1* was a nearest neighbor to females more often than the highest-ranking male in the group, *R2*, in both post-migration, 1992 and post-migration, 1993 seasons. Male *R3* exhibited higher nearest neighbor rates to females during post-migration, 1992, and male *R5* during post-migration, 1993. In Green group, lower-ranking male *G2* was a nearest neighbor to females more often than high-ranking *G1* in all seasons except mating and post-migration, 1993. The lower-ranking male in Blue group exhibited higher nearest neighbor rates with females during post-migration, 1992, and gestation seasons compared with the higher-ranking male. The two males in this group exhibited a reversal of rank near the end of the gestation period.

#### REPRODUCTIVE SEASONALITY AND INTERMALE AFFILIATIVE BEHAVIOR

The frequency of affiliative behavior between *Lemur catta* males differed significantly across reproductive seasons (Friedman two-way analysis of variance,  $\chi^2=19.29$ ,  $df=4$ ,  $p<0.001$ ) see Figure 2. The male that died halfway through the study period (*R6*) was not included in this analysis.

In particular, males engaged in more friendly behaviors with each other during the lactation season. One possible explanation for such a trend may be that male dispersal occurs during the lactation season, and males who migrate together exhibit extremely high frequencies of affiliative behavior with each other. Male-male competition and agonistic interactions peaked during mating season, and affiliative interactions were absent among some of the sample males.

#### MIGRATION IN THE STUDY GROUPS AND AFFILIATIVE BEHAVIOR OF IMMIGRATING MALES DURING THE MIGRATION PROCESS

Migration activity affected all three of the study groups in the 1991/1992 migration season. Based on migration data from the two years prior to my study (SUSSMAN, 1992;

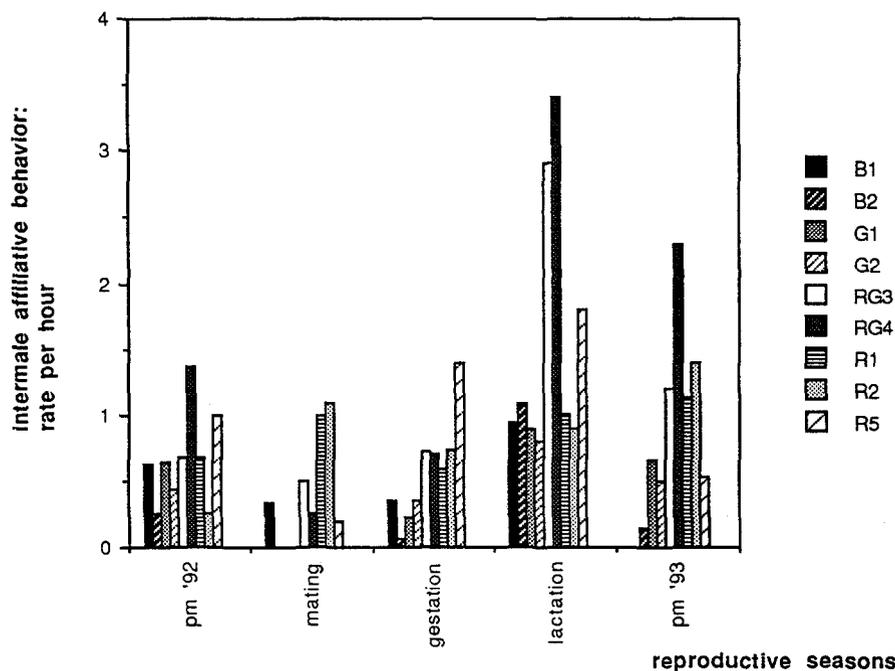
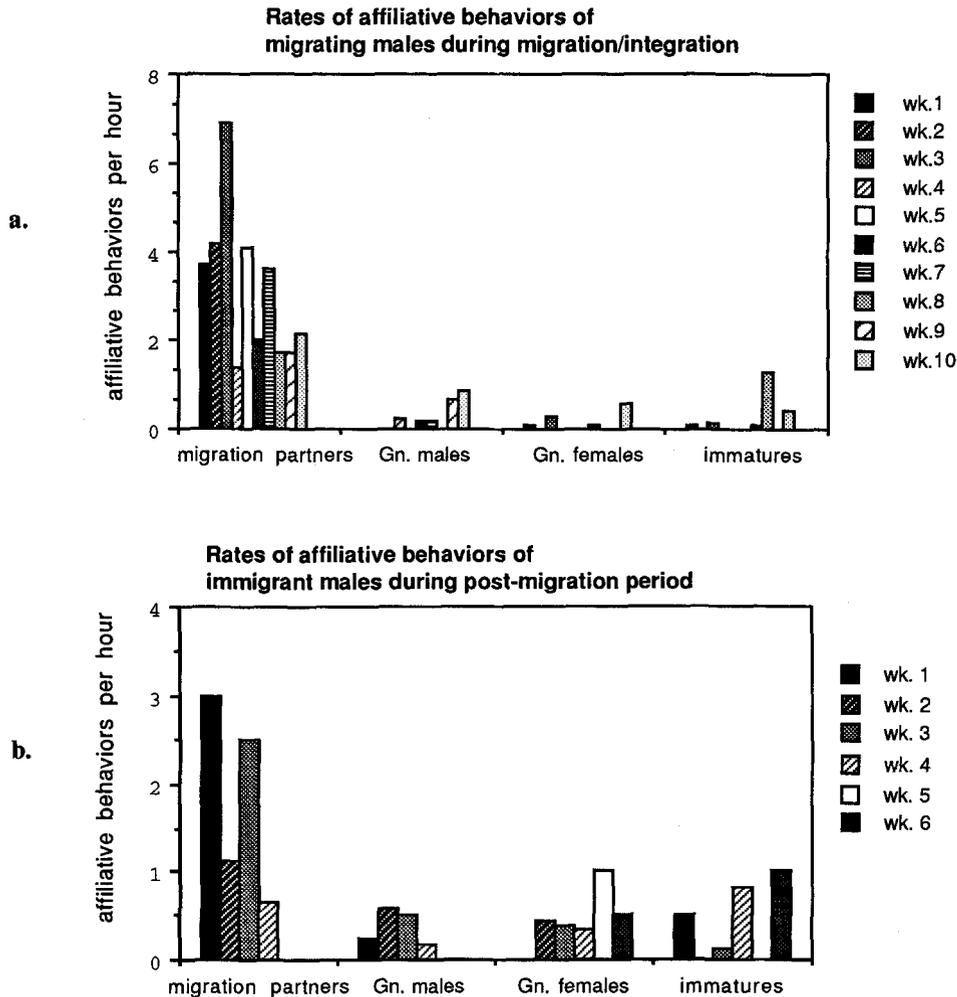


Fig. 2. Differences in intermale affiliative behavior in relation to reproductive seasons.

NASH, unpubl. census data), the two Blue group males had transferred into Blue from another group in the reserve just prior to the onset of my study; three males had transferred out of Green group during the 1991/1992 migration season, leaving the two focal males; and in Red group, two males had transferred out and four of the six focal males had transferred in during the 1991/1992 migration season.

During the 1992/1993 migration season, both immigration and emigration activity affected Red and Green groups. In late September 1992, males *R3* and *R4* began spending time on the periphery of and away from Red group during the day. By early November, the two males were spending most of their day with Green group, and by January they were integrated into the group. Figure 3a represents the hourly rate of affiliative behaviors between the two immigrating males (now *RG3* and *RG4*) and the Green group males and females during the ten-week immigration/integration period. The rates of the immigrant males' affiliative behavior with both males and females in the new group were very low or non-existent throughout the migration/integration period. Only during the final two weeks did the immigrants begin to affiliate somewhat more often with the resident Green group males. In only four of the ten migration weeks was any affiliation with females observed.

The post-immigration period occurred between January 26, 1993 and the end of the study period, March 13, 1993. In Figure 3b, I present the hourly rates of affiliative behaviors of the two immigrant males with other Green group members during the six-week post-immigration period. Frequencies of affiliative behavior between *RG3* and *RG4* decreased markedly from that observed during the migration season. During the last two weeks of the post-immigration period, no affiliative behavior was observed between the two



**Fig. 3.** **a.** Rates of affiliative behavior of migrating males during the immigration/integration period. Gn.males: Green group males; Gn.females: Green group females; **b.** Rates of affiliative behavior of the new immigrant males during the post-immigration period.

new immigrants. Although no affiliative behavior between the immigrants and adult females was observed during week one of the post-immigration period, they did engage in such interactions with the females between weeks two and six, and the rates were somewhat higher in weeks five and six than previously.

#### AN INTERMALE AFFILIATIVE RELATIONSHIP BETWEEN A SEVERELY INJURED MALE AND ANOTHER GROUP MEMBER

An affiliative partnership occurred between two males in Red group at the end of the mating season, and continued until the death of one of the males three months later.

Near the end of the mating season, male *R6*, an old animal, disappeared for four days. On June 10, he arrived back in Red group after much contact calling, with a badly injured leg. Male *R5*, a prime-aged male, approached him, and for several weeks the two males engaged in frequent bouts of affiliative behavior. Two weeks after the injury occurred, *R6* had licked and bitten all of the fur away from the site of the injury, and the end of the broken tibia emerged through the skin. He was not able to keep up with the group during progressions or feed in mid-to-high canopy. *R5* waited for him or contact called to him during group progressions. During the early stages of *R6*'s injury, *R5* kept within fairly close proximity to him. He continually approached *R6*, sat near him, or attempted to groom him; however, as time passed, *R6* became more and more peripheral to the group. *R5*'s attempts at affiliative behavior continued until the death of *R6* in mid-August. For a few weeks after his death, *R5* continued to contact call during group progressions. It is unlikely that these two males were related, as *R6* was one of the originally tagged animals, captured in 1987 (SUSSMAN, 1992), and had lived in the reserve at least five years, and *R5* had migrated into the Beza-Mahafaly population from outside of the reserve in 1992 (GOULD, unpubl. data).

## DISCUSSION

### ABSENCE OF RANK AND AGE EFFECTS IN INTERMALE PARTNERSHIPS

Unlike reports of intermale affiliation in female-bonded species such as rhesus and bonnet macaques, and South American squirrel monkeys, where males of similar dominance rank and age tend to affiliate most frequently (KAUFMANN, 1967; SILK, 1994; MITCHELL, 1994), males of all ranks and age-classes were observed to form affiliative preferred partnerships during the study period. Furthermore, none of the preferred partnerships were of a long-term nature. A number of factors might explain the absence of rank or age-related trends, and the brevity of these relationships.

First, numerous changes in the male dominance hierarchy occurred in all three study groups over the 12-month period. The dominance ranks of seven of the ten focal males (including the one that died during the study) either increased or fell from the rank they had exhibited at the onset of the study. The first nine months of this study occurred during a period of severe drought in the Beza-Mahafaly region. Food scarcity and high mortality among the reserve population (GOULD et al., 1996) may have affected the stability of male dominance ranks within the groups. A comparative study in a year when conditions are less harsh may yield differences with respect to the stability of the male dominance hierarchies.

Second, no evidence was found to support the hypothesis that lower-ranking males may attempt to form affiliative relationships with a higher-ranking males in order to be nearer to the female core of the group, as high-ranking males in my study were not the nearest neighbors to females more often than were lower-ranking males. This differs from SAUTHER'S (1991, 1992) observation of two groups at Beza-Mahafaly in 1988 where she found one "central non-natal male" in each group. She noted that such males could be differentiated by their closeness to the central female core of the group, and that they exhibited more frequent affiliative interactions with females. Clearly, variation occurs with respect to the dynamics of the adult males spatial and dominance structure within the Beza-Mahafaly population from one year to the next. Therefore, while it may conceivably benefit

a lower-ranking male to develop a partnership with a higher-ranking one in certain years, the data from the year of my study do not support this hypothesis.

Third, the mean number of males in the reserve population (8 groups) was 3.2 for 1992/1993. In most groups there were not enough adult males for partnerships to form among males of similar rank or age-class. In studies where rank and age patterns were found in male affiliative relationships, the groups studied were much larger than the *Lemur catta* groups at Beza, and contained many more males. For example in MITCHELL'S (1994) study of male South American squirrel monkeys, her sample size in one group was 50, and in SILK'S (1994) study of bonnet macaques, the sample size was 16 males in one group.

I suggest that these factors: fluctuation in the male dominance hierarchy, the drought that occurred during the study period, the fact that lower-ranking males had equal access to the female core of the group during the year of my study, and low numbers of males in each group may explain why no rank or age-related patterns were detected in male affiliative partnerships in the focal groups.

#### SHORT-TERM AFFILIATIVE PARTNERSHIPS

The brevity of intermale affiliative partnerships found in the study may have been influenced by male dispersal. Migration season in the reserve population can take place over six months of the year (SUSSMAN, 1992). Male dispersal activity over the 1991/1992 and 1992/1993 seasons resulted in either a complete change in male membership or marked differences in the male composition of the study groups. Such instability in the male membership of these groups might have had an effect on the length of affiliative partnerships. To further illustrate this point, I returned to Beza-Mahafaly in October 1994 to conduct a study of vigilance behavior in the same three groups, and found that only one of the nine focal males from the previous year (male *R1*) remained in the reserve population (males are able to disperse out of the reserve).

#### INTERMALE AFFILIATIVE BEHAVIOR OVER REPRODUCTIVE SEASONS

Few anthropoid primate species exhibit the type of strict reproductive seasonality seen in ringtailed lemurs. In the cases where data are available, some variation in intermale affiliation has been reported. For example, ROWELL and DIXSON (1975) found that male talapoin monkeys, which are usually spatially separate from females, joined all female sub-groups during mating season and did not associate with other males. In a group of Japanese macaques on Yakushima Island, FURUICHI (1985) reported that although resident males were intolerant and agonistic towards new males during the mating season, close associations formed between these males after the mating period. The sample males in my study engaged in significantly more affiliative behavior during the lactation period compared with the other reproductive seasons. Such a trend might be explained by the fact that male transfer occurs concurrently with lactation season, and that the migrating males exhibited extremely high rates of affiliative behavior with each other at this time. It should also be noted, however, that a number of resident males in the sample also exhibited high rates of intermale affiliative behavior during both lactation and post-migration, 1993 periods. Such a high frequency of affiliative behavior between the migrating males could be regarded as a confounding variable when attempting to make comparisons between intermale affiliation over reproductive seasons. However, male dispersal is a part of the life

history pattern of *Lemur catta*, and because males often transfer in pairs or small groups (JONES, 1983; SUSSMAN, 1992, pers. obs.), and since immigration into a new group can take several months, I suggest that such a trend can be considered an aspect of the behavioral repertoire found in this species, and not a confounding variable. Another possible explanation for higher levels of intermale affiliation during lactation season might have been that female involvement with infants could reduce the availability of females as affiliative partners; however, no decrease was found in the rate of male-female affiliative behavior during the lactation period compared with other reproductive seasons (GOULD, 1996).

#### BEHAVIOR OF DISPERSING MALES

Although dispersing males tend to form partnerships during migration season (JONES, 1983; SUSSMAN, 1992, pers. obs.), male coalitions and alliance behavior during migration, such as that observed in some macaque and baboon species, and in South American squirrel monkeys (MEIKLE & VESSEY, 1981; SPRAGUE, 1992; NOE, 1992; MITCHELL, 1994) has not been reported in ringtailed lemurs. In the first intensive study of ringtailed lemurs, JOLLY (1966) noted that she found no tendency for adult males to mutually defend one another. Although the two immigrant males in my study were subject to agonistic behavior such as chasing and stink-fighting from the two resident males in Green group during the immigration period, I did not observe any type of intervention or support by one or the other in such instances. However, even though intervention in agonistic disputes has not been reported, SUSSMAN (1992) suggests that because dispersing males are subject to attack by resident males, males transferring in pairs or triplets are in a better position to spot and defend themselves against such attacks than if a male was migrating alone.

One suggested function of male transfer partnerships is predator protection and detection of attack by resident males (SUSSMAN, 1992). SUSSMAN (1991) argued that lone dispersing males would be highly susceptible to predation and that such males would be likely to find one another and join together as a small group until the opportunity arose to migrate to heterosexual groups. On two occasions during the early immigration period, when male *RG4* left Red group and travelled to the periphery of other groups alone, my assistant and I observed him being targetted by a Madagascar harrier hawk (*Polyboroides radiatus*) while sitting at the top of a tree. Fortunately, he was able to drop from the high branches immediately and was not injured on either occasion. We did not observe such an interaction between a predator and either male when the two males were travelling together.

While migration partners can offer improved predator detection and protection, I also suggest that such partners are important in a social sense, as migrating males rarely socialize with other conspecifics during the actual immigration process. The two immigrant males in my study exhibited extremely high rates of affiliative behavior with one another during the entire immigration period. Only during the post-immigration period did they begin to interact less often with each other, and more frequently with Green group members, particularly with females and immatures.

#### CONCLUSIONS

FURUICHI (1985) argued that relationships among male Japanese macaques are influenced

by their affiliative relations with females. Both FURUICHI (1985) and HILL (1994) suggest that for male Japanese macaques, females are the preferred affiliative partners, and they found that when males were unable to affiliate with females, they formed affiliative partnerships with other males. I suggest that a similar trend exists in ringtailed lemurs. I propose that an integral aspect of male sociality and successful group membership relates to the development of social relationships with females (GOULD, 1994, 1996). Such relationships can result in closer spatial proximity to the core of the group, which can in turn lead to enhanced predator protection and greater opportunities for social contact with females, which could potentially result in improved access to estrous females during the mating period. When females are not available, males may form affiliative relationships with other males in the group, which do not appear to be influenced by male dominance rank or age. Such relationships can provide social benefits as well as health benefits such as ectoparasite control through allogrooming, and protection during the cold season through huddling and resting in contact. Migrating males benefit from high-level association with each other in terms of predator protection, and enhanced detection of attack by resident males, and they also provide reciprocal social contact during the migration period.

**Acknowledgements.** I thank Dr. R. W. SUSSMAN for his help and encouragement throughout this project. I also thank Drs. D. T. RASMUSSEN, J. PHILLIPS-CONROY, J. LOSOS, A. TEMPLETON, and Z. TANG-MARTINEZ, L. M. FEDIGAN and three anonymous reviewers for their helpful comments on earlier drafts of this manuscript, I am extremely grateful to Mme. BERTHE RAKOTOSAMIMANANA, M. POTHIN RAKOTOMANGA, Dr. ANDRIANANSOLO RANAIVOSON, M. BENJAMIN ANDRIAMIHAJA, MME. CELESTINE RAVAOARINOROMANGA, the School of Agronomy at the University of Antananarivo, and Direction des Eaux et Forêt, Madagascar for granting me permission to conduct research at the Beza-Mahafaly Reserve. Special thanks to JONAH RATSIMBAZAFY, for his excellent research assistance. This research was funded by a National Science Foundation Dissertation Improvement Grant (No. BNS-9119122), a Wenner-Gren Pre-doctoral Research Grant (No. 5401), a National Geographic Research Grant (No. 4734-92), a research grant from the Boise Fund of Oxford, and a scholarship from the Alberta Heritage Foundation.

## REFERENCES

- ALTMANN, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, 49: 227–265.
- BALDWIN, J. D. 1968. The social behavior of adult male squirrel monkeys in a semi-natural environment. *Folia Primatol.*, 9: 281–314.
- BUDNITZ, N.; DAINIS, K. 1975. *Lemur catta*: ecology and behavior. In: *Lemur Biology*, TATTERSALL, I.; SUSSMAN, R. W. (eds.), Plenum Press, New York, pp. 219–235.
- CHENEY, D. L. 1983a. Extrafamilial alliances among vervet monkeys. In: *Primate Social Relationships: An Integrated Approach*, HINDE, R. A. (ed.), Oxford Press, Blackwell, pp. 278–286.
- CHENEY, D. L. 1983b. Proximate and ultimate factors related to the distribution of male migration. In: *Primate Social Relationships: An Integrated Approach*, HINDE, R. A. (ed.), Oxford Press, Blackwell, pp. 241–249.
- DRICKAMER, L. C.; VESSEY, S. H. 1973. Group changing in free-ranging rhesus monkeys. *Primates*, 14: 359–368.
- FURUICHI, T. 1985. Inter-male associations in a wild Japanese macaque troop on Yakushima Island, Japan. *Primates*, 26: 219–237.
- GOULD, L. 1989. Infant social development and alloparenting in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. M.A. thesis, Univ. of Alberta, Alberta.
- GOULD, L. 1994. Patterns of affiliative behavior in adult male ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. Ph.D. diss., Washington Univ., Missouri.

- GOULD, L. 1996. Male-female affiliative behavior in naturally occurring ringtailed lemurs (*Lemur catta*) at Beza-Mahafaly Reserve, Madagascar. *Amer. J. Primatol.*, 39: 63–78.
- GOULD, L.; SUSSMAN, R. W.; SAUTHER, M. L. 1996. Demographic patterns from a long-term study of ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. Paper presented at the 16th Congress of the International Primatological Society, Madison, Wisconsin, August 11-16, 1996.
- HARDING, R. S. O. 1980. Agonism, ranking, and the social behavior of adult male baboons. *Amer. J. Phys. Anthropol.*, 53: 203–216.
- HASEGAWA, T.; HIRAIWA, M. 1980. Social interactions of orphans observed in a free-ranging troop of Japanese monkeys. *Folia Primatol.*, 33: 129–158.
- HILL, D. A. 1994. Affiliative behaviour between adult males of the genus *Macaca*. *Behaviour*, 130: 294–308.
- HILL, D. A.; VAN HOOFF, J. A. R. A. M. 1994. Affiliative relationships between males in groups of nonhuman primates: a summary. *Behaviour*, 130: 143–149.
- JOLLY, A. 1966. *Lemur Behavior*. Univ. of Chicago Press, Chicago.
- JOLLY, A. 1967. Breeding synchrony in wild *Lemur catta*. In: *Social Communication Among Primates*, ALTMANN, S. A. (ed.), Univ. of Chicago Press, Chicago, pp. 3–14.
- JOLLY, A. 1972. Troop continuity and troop spacing in *Propithecus verreauxi* and *Lemur catta* at Berenty (Madagascar). *Folia Primatol.*, 17: 335.
- JOLLY, A. 1984. The puzzle of female feeding priority. In: *Female Primates: Studies by Women Primatologists*, SMALL, M. F. (ed.), Alan R. Liss, New York, pp. 197–215.
- JONES, K. C. 1983. Inter-troop transfer of *Lemur catta* males at Berenty, Madagascar. *Folia Primatol.*, 40: 145–160.
- KAUFMANN, J. H. 1967. Social relations of adult males in a free-ranging band of rhesus monkeys. In: *Social Communication Among Primates*, ALTMANN, S. A. (ed.), Univ. of Chicago Press, Chicago, pp. 73–98.
- LINDBERG, D. G. 1973. Grooming behavior as a regulator of social interactions in rhesus monkeys. In: *Behavioral Regulators of Behavior*, CARPENTER, C. R. (ed.), Bucknell Univ. Press, Lewisburg.
- MEIKLE, D. B.; VESSEY, S. H. 1981. Nepotism among rhesus monkey brothers. *Nature*, 294: 160–161.
- MERTLE-MILHOLLEN, A. S.; GUSTAFSON, H. L.; BUDNITZ, N.; DAINIS, K.; JOLLY, A. 1979. Population and territory stability of the *Lemur catta* at Berenty, Madagascar. *Folia Primatol.*, 31: 106–122.
- MITCHELL, C. L. 1994. Migration alliances and coalitions among adult male South American squirrel monkeys (*Saimiri sciureus*). *Behaviour*, 130: 169–190.
- NOE, R. 1992. Alliance formation among male baboons: shopping for profitable partners. In: *Cooperation in Conflict: Coalitions and Alliances in Animals and Humans*, HARCOURT, A. H.; DE WAAL, F. B. M. (eds.), Oxford Univ. Press, Oxford, pp. 285–322.
- PEREIRA, M. E.; KAUFMANN, R.; KAPPELER, P. M.; OVERDORFF, D. J. 1990. Female dominance does not characterize all of the Lemuridae. *Folia Primatol.*, 55: 96–103.
- RANSOM, T. W. 1981. *Beach Troop of Gombe*. Associated University Press, New Jersey.
- RICHARD, A. F. 1987. Malagasy prosimians: female dominance. In: *Primate Societies*, SMUTS, B. B.; CHENEY, D. L.; SEYFARTH, R. M.; WRANGHAM, R. W.; STRUHSAKER, T. T. (eds.), The Univ. of Chicago Press, Chicago, pp. 25–33.
- ROWELL, T. E.; DIXSON, A. F. 1975. Changes in social organization during the breeding season of wild talapoin monkeys. *J. Reprod. Fertil.*, 43: 419–434.
- SAAYMAN, G. S. 1971. Behavior of the adult males in a troop of free-ranging chacma baboons (*Papio ursinus*). *Folia Primatol.*, 15: 36–57.
- SAUTHER, M. L. 1991. Reproductive behavior of free-ranging *Lemur catta* at Beza-Mahafaly Special Reserve, Madagascar. *Amer. J. Phys. Anthropol.*, 84: 463–477.
- SAUTHER, M. L. 1992. The effect of reproductive state, social rank and group size on resource use among free-ranging ringtailed lemurs (*Lemur catta*). Ph.D. diss., Washington Univ., Missouri.
- SAUTHER, M. L.; SUSSMAN, R. W. 1993. A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In: *Lemur Social Systems and Their Ecological Basis*, KAPPELER, P. M.; GANZHORN, J. U. (eds.), Plenum Press, New York, pp. 111–121.
- SILK, J. B. 1994. Social relationships of male bonnet macaques: male bonding in a matrilineal society. *Behaviour*, 130: 271–291.

- SLATER, P. J. B. 1978. Data collection. In: *Ethology*, COLGAN, P. W. (ed.), Wiley, New York, pp. 7–24.
- SMUTS, B. B. 1985. *Sex and Friendship in Baboons*. Aldine Press, New York.
- SMUTS, B. B.; WATANABE, J. M. 1990. Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). *Int. J. Primatol.*, 11: 147–171.
- SPRAGUE, D. S. 1992. Life history and intertroop mobility among Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.*, 13: 437–454.
- SUGIYAMA, Y. 1976. Life history of male Japanese monkeys. In: *Advances in the Study of Behavior*, Vol. 7, ROSENBLATT, J. A.; HINDE, R. A.; SHAW, E.; BEER, C. (eds.), Academic Press, New York, pp. 255–285.
- SUSSMAN, R. W. 1977. Socialization, social structure and ecology of two sympatric species of *Lemur*. In: *Primate Bio-social Development*, CHEVALIER-SKOLNIKOFF, S.; POIRIER, F. (eds.), Garland Press, New York, pp. 515–529.
- SUSSMAN, R. W. 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza-Mahafaly Reserve, Madagascar. *Amer. J. Phys. Anthropol.*, 84: 43–58.
- SUSSMAN, R. W. 1992. Male life histories and inter-group mobility among ringtailed lemurs (*Lemur catta*). *Int. J. Primatol.*, 13: 395–413.
- TAYLOR, L. L. 1986. Kinship, dominance, and social organization in a semi-free-ranging group of ring-tailed lemurs (*Lemur catta*). Ph.D. diss., Washington Univ., Missouri.
- TAYLOR, L. L.; SUSSMAN, R. W. 1987. A preliminary study of kinship and social organization in a semi-free-ranging group of *Lemur catta*. *Int. J. Primatol.*, 6: 601–614.

— Received: November 27, 1995; Accepted: July 18, 1996

Author's Name and Present Address: LISA GOULD, *Department of Anthropology, University of Alberta, Edmonton, Alberta T6G 2H4, Canada.*