

# 16

## Male and Female Ringtailed Lemurs' Energetic Strategy Does Not Explain Female Dominance

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### 16.1. Introduction

Female dominance in terms of female feeding priority and female mate choice is characteristic of many lemur species. (Pollock, 1979; Jolly, 1984; Richard 1987; Kappeler, 1993; Meyers and Wright, 1993; Radespiel and Zimmermann, 2001). Female dominance is also found in *Pan paniscus* (Stanford, 1998). Malagasy Lemurs do not show any sexual dimorphism (Kappeler, 1991), while male bonobo weigh more than females. It seems that the dominance of one sex within a primate social group does not always depend on the weight.

Jolly (1984), Young et al. (1990), Pereira (1999), and Wright (1999) suggest as a hypothesis that female dominance is determined by important energy constraints during seasonal reproductive periods. Available energy is also seasonal and may be insufficient to satisfy the increased needs of the organism due to a very high rate of growth of the embryo and the infant.

In contrast, Kappeler (1996) observed that captive lemur mothers do not undergo any higher energy constraints than that of prosimians with no female dominance. In the same vein, Tilden et al. (1997) and von Engelhardt et al. (2000) have not found any obvious arguments to support a high rate of maternal investment during reproduction in lemur species. Embryo growth rate is not high during the gestation period, and the milk is neither richer nor of greater quantity than that of other prosimians, even in conditions of intense feeding competition. Finally, Sauther (1992) and Hemingway (1999) found no sexual differences in the activity budget and the feeding duration of *Lemur catta* and *Propithecus diadema edwardsi*. However, the latter showed a difference in the dietary composition of males and females, because females chose some differing plant parts during the lactation period.

Thus, according to Kappeler (1996), Malagasy primate female dominance would not directly depend on their physiological state (estrus, gestation, and lactation) given the results obtained from captive animals. This author concludes that there is probably no reason to tie the physiology of reproduction to the social behavior, but that this interpretation should still be restudied in natural conditions with limited food. Therefore, I undertook to study energy

budgets of wild male and female ringtailed lemurs, to sort out the relationships between female dominance, social behavior, and the physiological state of lemurs.

I compared male and female ringtailed lemur behavior, diet quality, and energy expenditure, taking into account social status and interactions within the troop. The questions areas follow: Does male and female energy expenditure reflect intrasexual dominance hierarchies, and/or degree of female aggression toward males? And does male and female energy expenditure explain female dominance? Finally, what is the physical activity level, that is, the ratio of total energy expenditure to basal metabolism of male and female ringtailed lemurs as compared to that of other primates?

## 16.2. Methods

I compared 10 adult males and 10 adult females living in two different troops of *Lemur catta* in the Berenty Private Reserve, 25 °05' east and 46 °18,5' south (see Jolly *et al.* in this volume for a detailed description of the site). One of the two studied troops (troop D1A) was located in natural gallery forest and the second troop (troop G3) in the tourist area with introduced plants and garbage from the kitchen of the restaurant (see Rasamimanana and Rafidinarivo, 1993).

Focal sampling allowed us to observe each member of each group and to analyze individual characteristics that could influence the interaction between animals and that in turn defined the whole group behavior. Troop composition is shown in Tables 16.1 and 16.2.

In troop D1A during the 2002 lactation period, there were two adult males, and between 2002 lactation and 2003 mating periods two more immigrated. Then one of the two original males in the troop died before mating.

One of the dominant females, Diqua, mated on the same day as a subordinate one, Dana, but did not succeed in giving birth. During the gestation period, Diqua regressed in rank to become the most subordinate at the end of the study during 2003 lactation period when she was always beaten by the other females, even the subordinate one. Despite this fact, Diqua was one of the most dominant over males, as much so as Dido the new alpha female.

Within troop G3, no rank changes were seen, but the most dominant female, Antitra, died at the end of the study being about 15 years old. She was the eldest among the troop members and the mother of all the more dominant females. She had lost 3 offspring for two successive years, two infants and one subadult. She was also one of the females most dominant over males; the second one being the most subordinate female, Bobo, who lost her infant at the same period as Antitra. Male immigration was seen only during the mating period, when a new immigrant succeeded in being first to mate a subordinate primate female.

TABLE 16.1. Characteristics of adult animals of D1A troop.

Lactation period	Diqua Female Dominant Lactating Dominant one of the latest to mate	Dido Female Dominant Lactating Dominant the second to mate	Doso Female Subordinate Lactating Dominant the first to mate	Dana Female Subordinate Lactating Subordinate one of the latest to mate	Deba Male Dominant Dominant The latest to mate with Dido, and Diqua, and Dana Dominant	Scar Male Dominant Dead 04/21/03 in the morning	Star Subordinate Male second to mate with Doso took off the mating cork Subordinate	Doma Subordinate Male first to mate with Doso
2002 Lactation period								
2003 Mating								
Gestation	Subordinate nongestating	Alpha dominante Gestating	Dominant Gestating	Subordinate Gestating	Dominant	Dead	Subordinate	Subordinate
Birth	Subordinate	Dominant Gave birth	Dominant Gave birth	Subordinate Gave birth	Dominant	Dead	Subordinate	Subordinate
Lactation	Subordinate	Dominant Lactating	Dominant Lactating	Subordinate Lactating	Dominant	Dead	Subordinate	Subordinate

TABLE 16.2. Characteristics of adult animals of G3 troop.

2002 Lactation period	Antitra	Cœur	Tata	Mavo	Kello	Bobo	RE	Triangle	Rabiro	Point noir	LE	Telosof	Vakiampo
	Female	Subadulte Antitra's daughter	Female Antitra's daughter	Female	Female	Female	Male	Male	Male	Male	Male	Male	Male
	Equivalent rank	No lactating	Not followed	Subordinate lactating	No lactating	Subordinate lactating	Dominant	Not yet in troop	Subordin.	Subordin.	Subordin.	Subadult not followed	Subordin.
2003 Mating	Dominant not observed to mate	Primipare Dominant first to mate	Dominant not observed to mate	Subordinate ordinate observed to mate	Subordinate not to mate Peripheral	Sub-first second observed to mate	Dominant to not mate with Ceur took off the Kello.	Immigrant Subordin. First to mate with Kello.	Subordin. peripheral	Subordin. peripheral	Subordin.	Subordin.	Subordin. third to mate with Kello
Gestation	Dominant gestating	Dominant alpha Gestating	Dominant Gestating	Subordinate Gestating	Subordinate Gestating	Subordinate Gestating	Dominant Kello	Subordin.	Subordin. Peripheral	Subordin. Peripheral	Subordin.	Subordin.	Subordin.
Birth	Dominant last to give birth, lost its infant at the second day	Dominant First to give birth	Dominant Second to give birth	Subordinate Fourth to give birth	Subordinate Third to give birth	Subordinate fifth to give birth, lost its infant at the fifth day	Dominant	Subordin.	Subordin. Peripheral	Subordin.	Subordin.	Subordin.	Subordin.
Lactation	Died 10/25/03 late morning, 3 days after its subadult son	Dominant lactating	Dominant lactator/din.	Subordinate lactating	Subordin.	Subordin.	Dominant	Subordin.	Subordin. Peripheral	Subordin. Peripheral	Subordin.	Subordin.	Subordin.

### 16.2.1. *Behavioral Observations*

Individual troops were followed continuously through out the day from 0600 to 1800 h, with a break from 1200 to 1400 h, because the animals mostly sleep in that interval of time (Rasamimanana and Rafidinarivo, 1993; Ramasiarisoa, 2000), during 1502 hours of observation spread across the four reproductive periods (mating, gestation, birth, and lactation) between October 2002 and November 2003. More details on the divisions of these periods are presented in Rasamimanana and Rafidinarivo (1993).

The activity of the animals was recorded using instantaneous scan sampling and focal animal sampling (Altmann, 1974). Data collected with instantaneous scan sampling every five minutes included troop activities such as sleeping, sunning, resting, foraging, grooming, moving and traveling, type of food consumed (plant species and its part), and location of the troop within  $25 \times 25$  m quadrats on a map of the study area (Williams, 1998). Scan sampling was conducted once a week in both troops (i.e., for 180 hours each troop). Data collected with focal animal sampling included the preceding activities, the duration of feeding of each individual on a particular plant food and its parts, the number of steps, jumps and leaps in order to calculate the distance covered during moving. This last was also estimated by GPS during traveling over a relatively long distance. Focal samples were 5 minutes long, but with three samples taken consecutively on each individual to minimize lost data. On average each individual was focal sampled for 45 hours valid for analysis in D1A troop and for 29 hours in G3 troop.

Using the duration of feeding it was possible to quantify the proportion of each food item that made up the ringtailed lemur diet. Activities were standard as in other primate studies, except that moving was defined as displacement over less than three meters, (thus usually within a single food patch.) Traveling was defined as displacement beyond 3 m. For calculation of total activity versus inactivity, sleeping, resting, and sunbathing were classed as inactivity, and feeding, moving, traveling, and grooming classed as activity.

Dominance within each sex was calculated by direction of aggression and submission, as is usual in primate studies. This does not describe individual relations between sexes, because in ringtailed lemurs all adult females dominate all adult males. Dominance between sexes was therefore defined by the frequency of aggression shown by each individual female toward all the males. So females were categorized in two groups: those more aggressive toward males and those less.

Binoculars,  $8 \times 30$  with  $7.5^\circ$  field, a GPS device and a compass, pen and paper were used to collect these data.

### 16.2.2. *Energy Expenditure*

Coelho (1974) uses the term socio-bioenergetics to indicate the study of the energy expenditure of an animal as a group member interacting within that group. The study rests on the basis of combination of physiological principles and

ethological techniques. By means of a “factorial” approach, the metabolic cost of an activity is related to the time each individual spent on it. This time is known from continuous focal observation of the animal. Coelho et al. (1976) established some indexes “K” of energy expenditure for each main activity (Table 16.3) of the animal which are used in allometric equation to calculate the energy expenditure of male and female *Lemur catta*.

Total energy expenditure in multiples of basal metabolism is calculated:

$$\text{Total energy expenditure TEE} = \sum_i^n C_i$$

- $C_i = K_i \text{ BMT}_i$  = energy expended for an activity “i” by a ringtailed lemur individual within a 10-h observation day.
- $K_i$  = index of energy expenditure for an activity “i” (Table 16.3), other than traveling. Traveling is calculated by another allometric equation below so does not have an index “K.”
- $T_i$  = time (hours) spent by a ringtailed individual for an activity “i” within a 10 h observation day.
- $\text{BM}$  = basal metabolism of *Lemur catta* predicted from Kleiber’s formula (1961)  $\text{MB} = 70W^{0.75}$  adjusted for lemur species. Kleiber’s calculated basal metabolism was reduced to 65% of its value according to the results obtained by Daniels (1984), Richard and Nicoll (1987), and Dracks et al. (1999), respectively, on *Eulemur fulvus* ssp., *Propithecus verreauxi verreauxi*, and *Lepilemur ruficaudatus*, who showed that prosimians have a much lower basal metabolism than other primates. Furthermore, it is known that the metabolism of a gestating and lactating mammal is respectively 1.25 times and 1.5 times higher than that of nongestating and nonlactating mammal (Crampton and Lloyd, 1959; Portman, 1970, in Coelho, 1974) so the theoretical values of basal metabolism of females were raised depending on their reproductive state.
- $W$  = weight. I attributed to every male the same average weight ( $W = 2.6 \text{ Kg}$ ) obtained from other individuals of adjacent troops weighed in March 2003 (Crawford et al., pers. comm.). The same process was done with the females ( $W = 2.3 \text{ kg}$ ) except for one individual we could weight ( $W = 1.750 \text{ kg}$ ), who died during the study.

TABLE 16.3. Indexes of energy expenditure for some ring-tailed activities.<sup>a</sup>

Activities	Index of energy expenditure (K)
Sleeping	1.00
Sunning and resting	1.25
Feeding	1.38
Grooming	2.35

<sup>a</sup> Values taken from Leonard and Robertson (1997).

The allometric equation calculating the energy spent during traveling is following:

$$C_{\text{travel}} = (0.041 W^{0.6}) DC + (0.029 W^{0.75}) T_{\text{travel}} = \text{energy expended by a ringtailed individual for traveling within a 10-h observation day (Leonard and Robertson, 1997).}$$

- W = weight (g) from Crawford et al. in this volume, as above.
- $T_{\text{travel}}$  = time spent for traveling by a lemur individual within a 10-h observation day (hours).
- DC = distance covered by a lemur individual within a 10-h observation day (km). This was estimated by GPS or calculated by the following formula:

$$DC = (23.10^{-5} \Sigma S) + (50.10^{-5} \Sigma J) + (10^{-3} \Sigma L)$$

where S = number of steps during traveling, J = number of jumps during traveling, and L = number of leaps during traveling.

The physical activity level (PAL) is calculated as TEE/BM. This allows a comparison of activity alone without the influence of the animal's weight or reproductive state (Leonard and Robertson 1997).

### 16.2.3. Statistical Analyses

We performed all statistical tests via Statistica 6.0 (Statsoft). As samples were not large, we mostly used non-parametric tests including chi-square test to estimate the dependence between the distributions of 10-h-daily inactivity and the physiological periods, the intrasexual hierarchy, the female dominance over males, and the sexes.

The parametric tests Student t-test was used to test the differences between energy expenditure and physical activity level of males and females and ANOVA to test the differences of energy expenditure and physical activity level within reproduction periods.

## 16.3. Results

### 16.3.1. Male and Female Activities and Inactivity

In order to sort out whether male and female energy expenditure could explain the female dominance in ringtailed lemurs, we calculated both sexes' daily distribution of activities at each reproductive period, mating, gestation, lactation and birth.

There was no difference between troops, so results from both troops are combined.

*Lemur catta* as a species spends most of its time at rest which matches with the fact it has a low basal metabolic rate (Daniels, 1984; Richard and Nicoll, 1987). Feeding, moving, traveling, and grooming could be gathered in one category

called activity, and the remaining three activities: sleeping, sunbathing and resting in another one called inactivity.

*Lemur catta* at every reproductive period more was inactive than active (Figure 16.1). However, during the mating and gestation periods the animals were more active than during birth and lactation. This due to the fact that males and females are mixed here, and feeding is a component of activity. While feeding during those two periods, they did more moving than during birth and lactation and more grooming while resting.

During mating and lactation periods, females were significantly more active than males (respectively mating:  $\chi^2 = 6.8$ ;  $df = 1$ ;  $p < 0.05$  and lactation:  $\chi^2 = 5.7$ ;  $df = 1$ ;  $p < 0.05$ ) (Figures 16.2 and 16.3). The big differences drawn in Figure

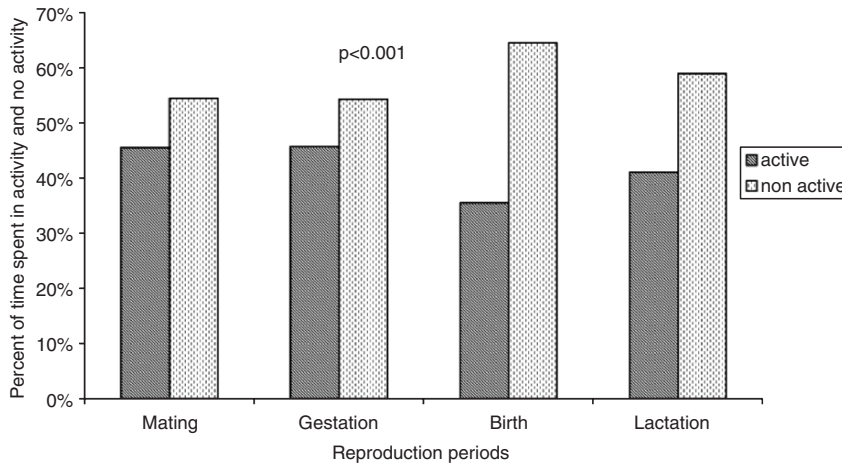


FIGURE 16.1. Inactivity of the animals during each reproductive period.

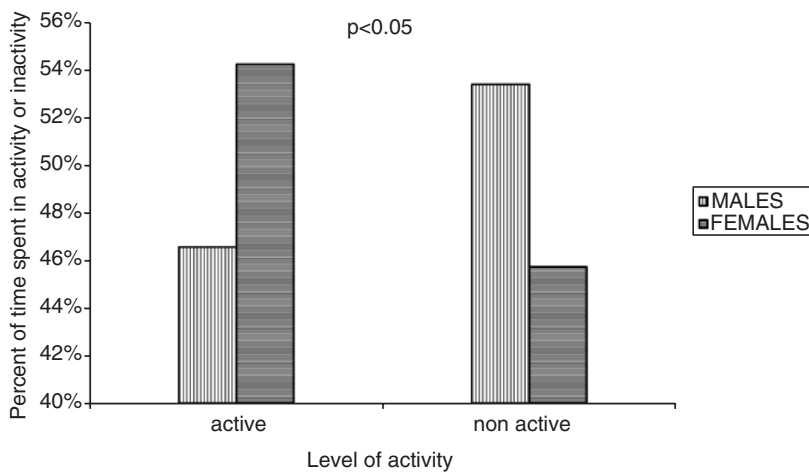


FIGURE 16.2. Level of activity of male and female *Lemur catta* during the mating period.



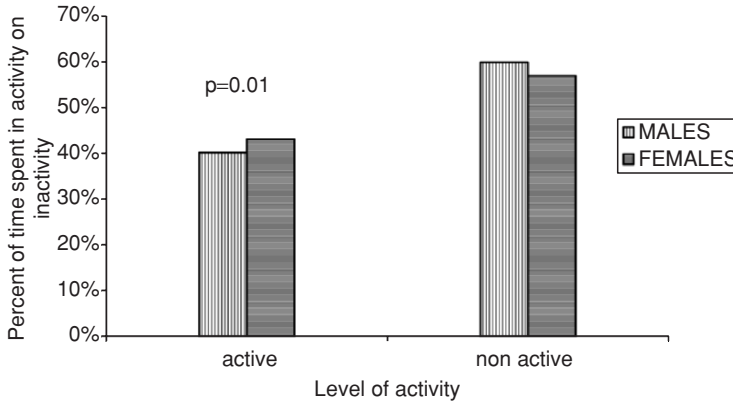


FIGURE 16.3. Level of activity of male and female *Lemur catta* during the lactation period.

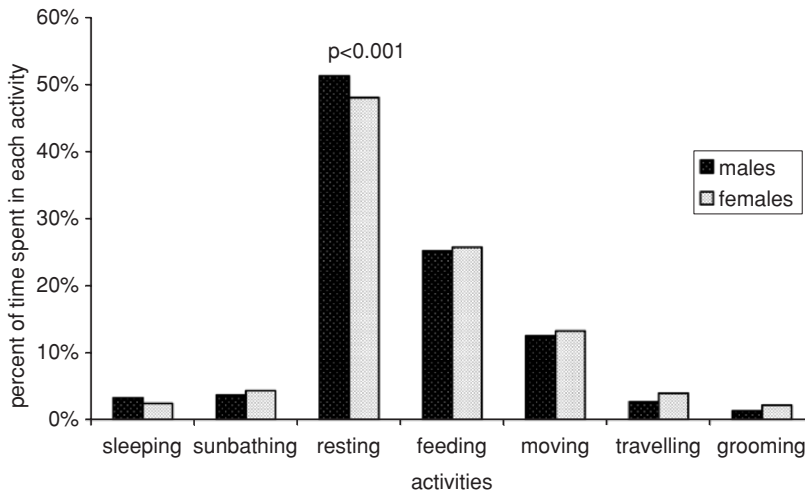


FIGURE 16.4. Percent of time animals spent in each activity according to their sex.

16.2 despite the fact that the difference is only significant at  $p < 0.05$  is probably due to the different number of samples obtained during the two periods. The numbers of observation days are less in the mating period than in lactation period due to the different length of those two periods.

This greater activity of females also appears as an overall difference between males and females in percent of time they spent in resting. Males rested statistically longer than females, and females moved, traveled and groomed more than males ( $\chi^2 = 11.17$ ;  $df = 6$ ;  $p < 0.001$ ) (Figure 16.4).

The components of activity differed according to the reproductive periods. Figure 16.5 shows that females spent more time in feeding during the gestation

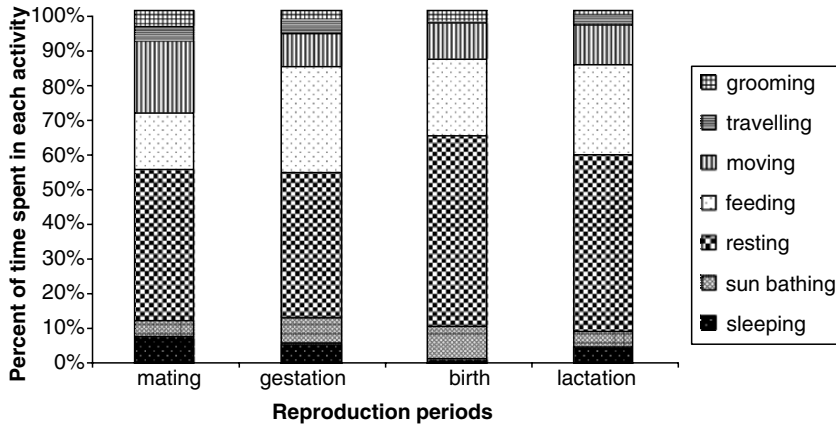


FIGURE 16.5. Distribution of female activities according to reproductive periods.

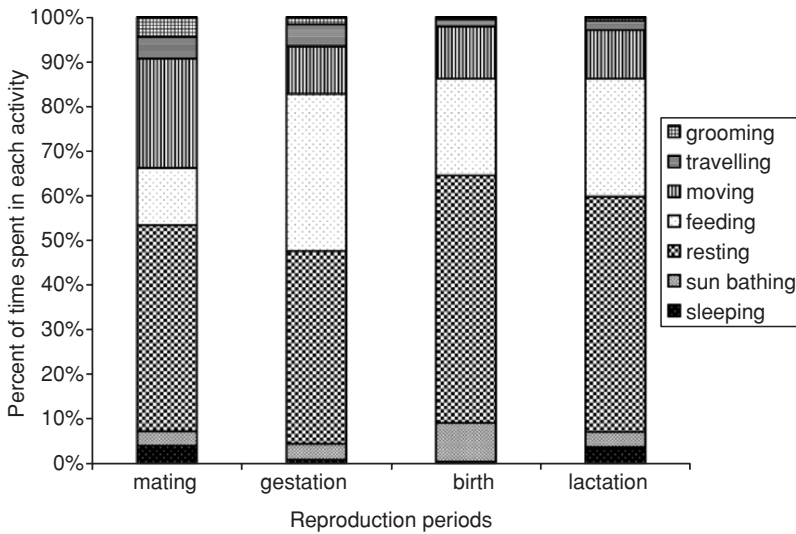


FIGURE 16.6. Distribution of male activities according to reproductive periods.

period and less time during mating period, while they were moved and travelled less during gestation and more during mating. Males displayed the same tendencies (Figure 16.6) during the gestation period, but during the birth period they traveled more than females.

### 16.3.2. *Level of Females' Activity in Relation to Their Dominance*

All females, whether dominant or subordinate in the female hierarchy, are dominant over males. In each study troop, the alpha and the most subordinate female

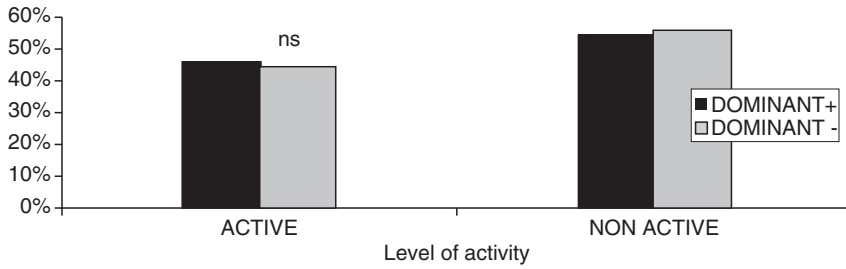


FIGURE 16.7. Percent of time females spent in inactivity in regard to their dominance over males.

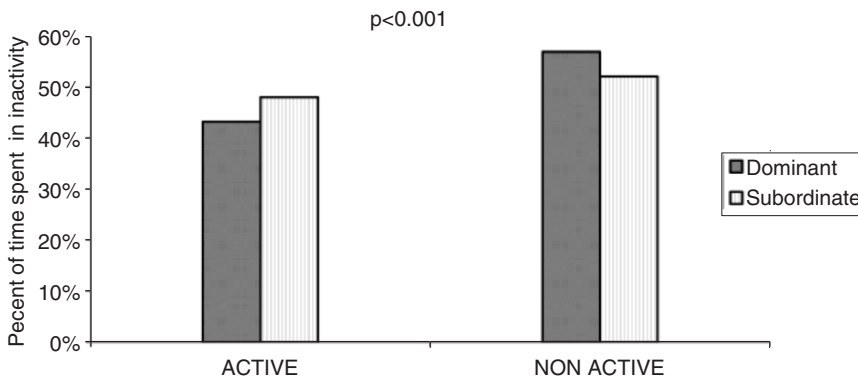


FIGURE 16.8. Percent of time spent in inactivity by females in regard to their intrasexual hierarchy.

were the most dominant over males as measured by frequency of aggression toward males. Curiously, those occupying the intermediate rank were less aggressive toward males. Female dominance toward males did not correlate with time inactive ( $\chi^2 = 0.66$ ;  $df = 1$ ;  $p = 0.42$ ) (Figure 16.7).

When they were analyzed in regard to the female hierarchy, it appeared that subordinate females were significantly more active than dominants ( $\chi^2 = 12.4$ ;  $df = 1$ ;  $p < 0.001$ ) (Figure 16.8).

On the other hand, the difference between dominants and subordinates in the male hierarchy was not significant ( $\chi^2 = 2.7$ ;  $df = 1$ ;  $p \geq 0.05$ ).

### 16.3.3. Male and Female Energy Expenditure

As mentioned above, energy expenditure depends on the animal's weight as well as its activity. The energy expenditure during 10-h-observation active day was calculated on the basis of Leonard and Robertson's (1997) formula taking in account the activities, the distance covered, and the basal metabolism of each individual.

No troop difference was observed in terms of energy expenditure of male and female *Lemur catta* of Berenty, so the data could be combined. The average distances covered by members of both troops during the focal observations were respectively 0.450 km during the mating period; 0.270 km during gestation period; 0.140 km during birth period, and 0.221 km during 2003 lactation period. This showed that the animals covered a longer distance during mating and gestation periods than during birth and lactation periods, both sexes combined.

Males' and females' energy expenditure varied from one reproductive period to another  $F(4.39) = 15.01$ ;  $p < 0.001$ . On average, females' energy expenditure showed a minimum of 82 kcal during the gestation period and a maximum of 104 kcal during the 2002 lactation period. In contrast, males had a minimum of 71 kcal during the 2003 lactation period and a maximum of 108 kcal during mating period. (Figure 16.9).

Activities counted as activity were feeding, moving, traveling, and grooming. The animals might spend a high percentage of time in those activities but covered a much shorter distance, so they might spend less energy, because total energy expended was significantly correlated with the distance covered ( $r = 0.71$   $p < 0.001$ ). Figure 16.10 showed that ringtailed females of both troops covered the longest distances during copulation and lactation periods. The maximum energy expended by females during the lactation period is explained by the long distance covered in short time and also by the fact that we multiply the basal metabolic rate of lactating females by 1.5, following Crampton and Lloyd (1959) and Portman (1970) in Coelho (1974).

Males and females expended their energy differently each from other during the mating ( $p = 0.02$ ) and lactation periods ( $p < 0.001$ ) (Figure 16.9). That could mean a high need by one sex or the other during those periods. Generally, the lac-

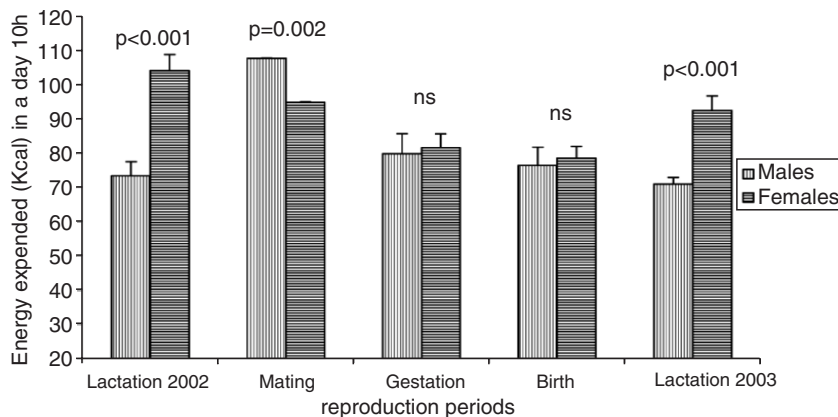


FIGURE 16.9. Energy expended on average in a 10-h-observation day by males and females during different reproductive periods.

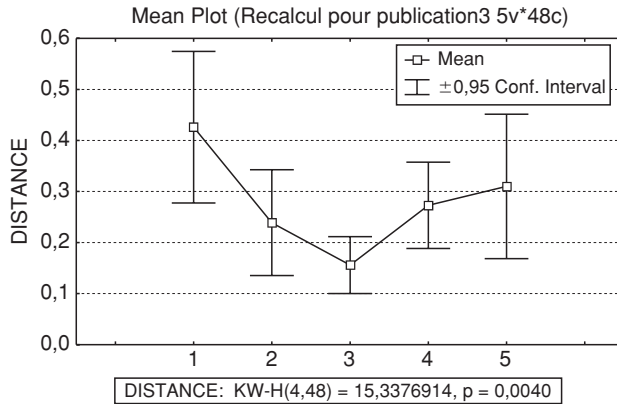


FIGURE 16.10. Mean distance covered by ring-tailed females during each reproductive period (1 = copulation period; 2 = gestation period; 3 = birth period; 4 and 5 = lactation periods in 2003 and 2002).

tation period is that of the highest energy expenditure for females and that of the least for males. On the contrary, the end of gestation to birth periods corresponded to the least energy expenditure for females (Figure 16.9) because of the short distance covered.

Sex and period influence on the energy expenditure were seen above, but there seemed not to be a significant intra-sexual hierarchy influence on this variable ( $p \geq 0.05$ ) (Table 16.4) due to the fact that the hierarchy status of the females was not steady in D1A troop during our observation study. A dominant female did not succeed in giving birth, which suggests she had already lost her position during the gestation period before parturition. Subordinate females expended more energy than dominants but that was not significant. If there is a difference between males and females but none within males or within females in regard to their hierarchy, what about female energy expenditure in regard to their dominance over males? There was no relationship between female dominance over

TABLE 16.4. Analysis of variance of the average energy expenditure (10-h observation) of ringtailed lemurs depending on the period, sex, and hierarchy intra-sexual.

	SS	Degrees of freedom	MS	F	p
Intercept	616589.9	1	616589.9	2912.511	0.000000
Period	7780.5	4	1945.1	9.188	0.000003
Hierarchy	128.0	1	128.0	0.604	0.439052
Sex	1263.4	1	1263.4	5.968	0.016639
Standard error	17994.8	85	211.7		

males and female energy expenditure even when the reproductive period and troop were taken in account ( $F(1, 41) = 0.16$ ;  $p = 0.69$  NS).

#### 16.3.4. *Male and Female Physical Activity Level*

The differences noted between males and females' energy expenditure was due either to their weight or to their activity differences. In order to compare individuals not taking their weight into account, one calculates the physical activity level (PAL), which is the ratio of the total energy expenditure to the basal metabolism.

As shown in Table 16.5, reproductive period influenced the PAL while troops, sex, and intrasexual hierarchy did not. The tendency effect of hierarchy is to be noted but was not significant. Although there was a significant difference between males' and females' energy expenditure, this was not the case for their physical activity level ( $F(1, 84) = 0.35$ ;  $p = 0.55$ ). Males and females were physically active at the same level during every reproductive period with no difference between troops.

The PAL of females more dominant toward males was statistically the same as that of females less dominant toward males.

When the females were analyzed by their intrasexual hierarchy, a difference in PAL was not statistically significant between dominant and subordinate females even though subordinate females had higher physical activity level than dominants (2.12 vs. 1.97). According to these results, it seemed that social group organization due to interactions within individuals did not have any direct relationship with the physical activity level of animals as Kappeler (1999) suggested. The females' PAL seemed neither to be linked to their social status nor to their reproductive state, for there was no significant difference between males' and females' PAL during gestation and lactation periods.

#### 16.3.5. *Individual Variation*

The variation between individuals was striking. Although many of the comparisons between males and females or between dominants and subordinates are not significant, individuals within each category could differ sharply. The variation of

TABLE 16.5. Analysis of variance of PAL according to the period, troop, sex, and intrasexual hierarchy.

	SS	Degrees of freedom	MS	F	p
Intercept	335.64	1	335.64	3963.46	<0.001
Period	10.81	4	2.70	31.94	<0.001
Group	0.014	1	0.014	0.16	0.68
Hierarchy	0.29	1	0.28	3.387	0.069
Sex	0.03	1	0.03	0.348	0.556
Standard error	7.11	84	0.08		

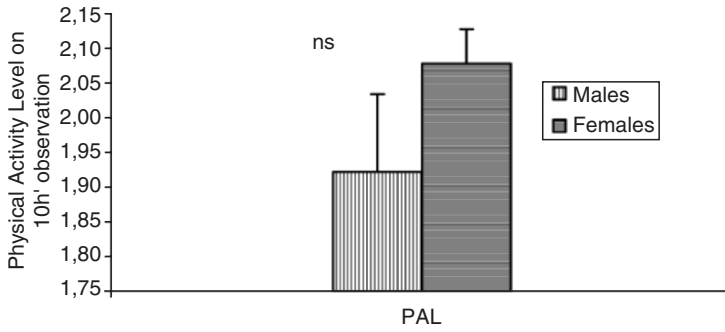


FIGURE 16.11. Comparison of the males and females' PAL in a 10-h day.

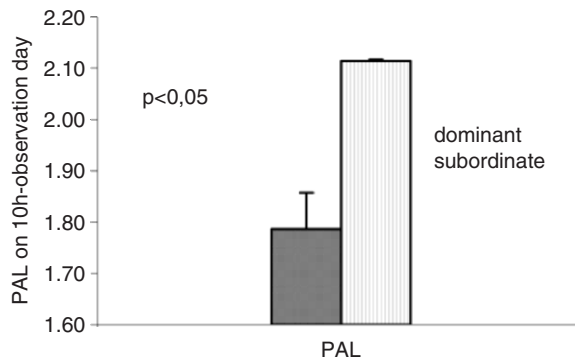


FIGURE 16.12. G3 troop females' PAL in respect to intrasexual hierarchy in a 10-h day during lactation, 2002.

the physical activity level between females was 2 times lower than that observed between males (Figure 16.11). During the 2002 lactation period, the variation of physical activity level among dominant troop G3 females was 7 times higher than among subordinate females (Figure 16.12). Individuality will be considered further in the discussion.

### 16.4. Discussion

At the present time, individual differences in non-human primate behavior, as well as that of other mammals, are being recognized and studied much more than in the recent past.

From this point of view, Lestel (2001) pointed out that ethological observations allow considering each animal as a subject having its own life history rather than

just as an object. This life history along with its individual genetic characteristics determines the gamut of its reactions to its group-mates. Recent work on anthropoids (Mitani et al., 2002) follows this course of analyzing the behavior of individuals, to show that they are aware of their relationships with other individuals in their troop.

Could it be possible to consider such a cognitive level in the lemurs of Madagascar, and up to what point, when there are clearly big differences in their learning ability from that of monkeys or apes (Wilkerson and Rumbaugh, 1979)? The study of primate social organization has progressed enormously, mainly with the study of Cercopithecidae (Kappeler and van Schaik, 2002), since Jolly (1966) first observed the *Lemur catta* troops, aspects of whose interindividual relationships are studied in the current work.

Before discussing energy expenditure and the physical activity level, one example among our observations on this lemur species will be enough to illustrate that among ringtailed lemurs, one individual may be totally different from another one.

That example concerns the parental investment of different individuals. One primiparous female of troop G3, called Coeur, daughter of a dominant female and dominant herself, gave birth to an infant in which she seemed to not invest much. Another female, Tata, Coeur's sister, apparently kidnapped her infant. Tata had already her own infant born some hours before that of Coeur. Both infants were hanging onto Tata's belly, and that of Coeur was suckling more often. An hour later, Coeur approached Tata, but Tata threatened her by staring and chased her away. Coeur ran away but came back several times trying unsuccessfully to pick up her infant. This process lasted 3 hours. Finally the infant was restored to Coeur with no aggression from Tata.

A few days later as the troop rested in the trees, each individual in contact with another, Coeur's infant jumped from one individual to the next. Coeur then rose up and left the troop. At any moment it seemed the infant might fall down. Tata and her mother Antitra both ran to retain it. Twenty minutes later Coeur was back, and the adult females made a contact call that could be interpreted as calling the "flighty mother."

Coeur's deficient parental investment continued over several more incidents. On one occasion the troop was feeding on garbage in an excavation and Coeur's infant was trying to climb down from its mother's back to explore its surroundings. A few minutes later, Coeur left the troop with other troop members without taking the baby on her back. The infant was not yet able to walk by itself so it was not able to get out of the excavation and it screamed. Its calls made an adult male come to it, threatening. A subadult male staying near the infant faced the adult male and made him leave. Twenty minutes later, the subadult took the screaming infant on its back and went toward the troop and the mother, but Coeur was high in the trees feeding and did not approach the new arrivals.

Tata and Antitra met them. The infant jumped right away to Antitra to suckle her. Twenty more minutes later Coeur climbed down the tree and came to the trio, but Tata rose up and cuffed her making her scream a submission call. During the



next 6 weeks of its life, the infant suckled alternatively its mother and Antitra whose own infant had died a few days after birth.

This kind of major difference between individuals' behaviors and between parental investments could partly explain the differences within males and females in regard to intrasexual hierarchy, daily distribution of activities, and physical activity level.

#### 16.4.1. *Interindividual Differences in Physical Activity Level*

Table 16.6 shows each individual PAL in both troops. The value of the average PAL was 2.09. A PAL above this value characterized the animal as more active and under it as less active. Only two males of the 11 observed were less active. Both belonged to G3 troop, one dominant and the second subordinate. Among females, 4 of 10 observed were less active and 3 of these were lactating and dominant. The difference between the lowest PAL of females (1.85) and males (1.96) during a 10-h day was not significant. That might be explained by the higher basal metabolism of the pregnant and lactating females we took in account during

TABLE 16.6. Individual classification by the average PAL according to the social status and the females reproductive state.

Subject	Sex	PAL average	Position in regard to the average	Social status	Females reproductive state
Deba	M	2.15	+	Dominant	
Star	M	2.12	+	Subordinate	
Doma	M	2.43	+	Subordinate	
Scar	M	2.15	+	Dominant	
RE	M	2.03	-	Dominant	
TR	M	2.1	+	Subordinate	
Rabistro	M	2.1	+	Subordinate	
Point noir	M	1.96	-	Subordinate	
LE	M	2.1	+	Subordinate	
Sofina	M	2.1	+	Subordinate	
Tatape	M	2.3	+	Subordinate	
Dido	F	2	+	Dominant	P.L
Doso	F	1.86	-	Dominant	P.L
Dana	F	1.99	-	Subordinate	P.L
Diqua	F	2.13	+	Subordinate	NP.NL.
Antitra	F	1.93	-	Dominant	P.L
Cœur	F	2.13	+	Dominant	P.L
Tata	F	1.85	-	Dominant	P.L
Mavo	F	2.1	+	Subordinate	P.L.
Kelilo	F	2.13	+	Subordinate	P.L
Bobo	F	2.34	+	Subordinate	P.NL.

P.L., pregnant and lactating; P.NL., pregnant and nonlactating; NP.NL., nonpregnant and nonlactating; +, more active; -, less active.

calculation of the PAL. Neither was there any significant difference between PAL of dominant and subordinate within sex, although one could think dominance status should be advantageous to obtain a high diet quality cheaply.

The difference between individual PALS did not seem to be related to female dominance over males. Indeed, Diqua and Dido of D1A troop had high PAL and were both the most dominant over males, while Antitra and Bobo, which were the most dominant over males in G3 troop, had the two extreme PAL values. But on the other hand, that also could suggest an absence of relationship between female dominance and reproductive state, for neither Diqua nor Bobo were lactating during the observation period.

#### 16.4.2. *Evolution and Energetic Strategy*

The most appropriate variable used to compare different species with respect to energetic strategy is the physical activity level, which does not take weight into account.

Data on *Lemur catta* displayed in Table 16.7 are those obtained by the current work using Leonard and Robertson's (1997) formula and doing the calculation on the basis of 24-h day to take in account the time spent sleeping. The PAL in 24h is 1.47 for males and 1.43 for females. *Lemur catta* is known as an animal with low basal metabolism, so it should be below Kleiber's regression line. To compare them with the other primate families that lie on Kleiber's regression line, we should make calculations that will elevate their basal metabolism. But if their Basal Metabolism is higher, it should enter both the total energy expenditure as higher and also the PAL, which is TEE/BM, so using a different BM should make little difference. Therefore they can be compared with those of other primate species, deduced from field work by different authors and reported in Leonard and Robertson (1997), in Warren and Crompton (1998) for other prosimian species, and in Dracks et al. (1999) for *Lepilemur ruficaudatus*.

Notably, among prosimians *Lemur catta* had the lowest PAL, with the highest weight. It had a less specialized diet than that of folivore *Lepilemur* and *Avahi*, or than that of insectivore *Tarsius* and *Galago* and the gummivore *Otolemur*. The high percent of time *Lemur catta* spends in resting could be explained by an energy saving strategy and folivore survival strategy. Indeed, leaves need a long time (around 5h in *Lemur catta*; Cabre-Vert and Feistner, 1996) to degrade the fibers almost entirely and to assimilate energy from that degradation.

Table 16.7 shows the high PAL of most prosimians correlated with their small size and thus their low total metabolism. Only the lorisidae, tarsiidae, and indriidae, with low basal metabolism, have PAL higher than 2. Thus, prosimians on the lowest level of the primate phylogenical scale and which had the best diet quality spent more energy for body size than other primates. From this

TABLE 16.7. Comparison of ringtailed lemur PAL with that of species from other families.

Species	Sex	Weight (kg)	PAL
LORISIDAE			
<i>Galago moholi</i>	M/F	0.182	4.9
<i>Otolemur crassicaudatus</i>	M/F	1.384	5.07
TARSIIDAE			
<i>Tarsius bancanus</i>	M/F	0.123	4.95
INDRIIDAE			
<i>Avahi laniger</i>	M/F	0.708	6.2
<i>Lepilemur edwardsi</i>	M/F	0.819	6.2
<i>Lepilemur ruficaudatus</i>	M	0.744	3.22
	F	0.747	2.8
LEMURIDAE			
<i>Lemur catta</i>	M	2.6	1.47
	F	2.3	1.43
CALLITRICHIDAE			
<i>Saguinus fuscicollis</i>	M/F	0.3	1.36
<i>Saguinus imperator</i>	M/F	0.4	1.29
CEBIDEA			
<i>Cebus apella</i>	M/F	2.6	1.29
<i>Cebus albifrons</i>	M/F	2.4	1.27
<i>Saimiri sciureus</i>	M/F	0.8	1.27
<i>Aotus trivirgatus</i>	M/F	0.85	1.50
<i>Callicebus moloch</i>	M/F	0.7	1.22
<i>Allouatta palliata</i>	M	8.5	1.18
	F	6.4	1.17
<i>Ateles geoffroyi</i>	M/F	8.41	1.20
CERCOPITHECIDAE			
<i>Cercocebus albigena</i>	M/F	7.9	1.31
<i>Macaca fascicularis</i>	M/F	5.5	1.19
<i>Papio anubis</i>	M	29.3	1.34
	F	13	1.34
<i>Colobus guereza</i>	M/F	7	1.24
HYLOBATIDAE			
<i>Hylobates lar</i>	M/F	6	1.17
<i>Siamea syndactylus</i>	M/F	10.5	1.23
PONGIDAE			
<i>Pan troglodytes</i>	M	39.5	1.46
	F	29.8	1.36
<i>Pongo pygmaeus</i>	M	83.6	1.33
	F	37.8	1.40
HOMINIDAE			
<i>Homo sapiens</i>			
!Kung	M	46	1.68
	F	41	1.56
Ache	M	59.6	2.00

viewpoint, they might have reached the upper limit of their physiological adaptability and might have an energy-limited way of life (Warren and Crompton, 1998).

If one compares species with female dominance or with no female dominance, it is noticeable that males' and females' PAL varies from 1.17 to 1.46 and that of males could be higher than that of females and vice versa. There is no relation of PAL to female dominance.

The other primates' species have a PAL between 1.68 and 1.17, similar to *Lemur catta*. There is no correlation between diet quality within this group and PAL ( $p = 0.2$ ).

In short, *Lemur catta* seems to be an exception as a prosimian. It has a folivorous–frugivorous diet, and its PAL matches with that of folivorous–frugivorous simians rather than the prosimians.

By my calculations, *Lemur catta* then seems to be at the limit allowed for energy expended in locomotion, which could explain the high percentage of time spent in inactivity during a 10-h day. Elsewhere its activity such as the sunbathing on waking allowed it to diminish the thermoregulation cost (Martin, 1974; Daniels, 1984; Peters, 1989). Its body temperature is also regulated by behaviors such as grouping together, one against another, in a big ball when the ambient temperature is cool, or on the contrary one away from another with spread limbs when the ambient temperature is hot. All these behaviors display a specific adaptational response to metabolic constraints.

## 16.5. Conclusion

Natural selection has presumably shaped the mechanism that ordered the social competition from which the dominance structure evolved. This competition would favor individuals with high degree of adaptation to their surroundings and with high degree of efficient reproduction of their genetic heritage.

Genes responsible for lemur female dominance may have come from a monogamous nocturnal lemur ancestor (van Schaik and Kappeler, 1996) especially because this behavior is observed in extant nocturnal lemurs when two different sexes encounter each other (Radespiel and Zimmermann, 2001, Dammhahn and Kappeler, 2005). Alternatively, they might come from pair-bonded—not exclusively nocturnal—ancestor (Jolly, 1998), whose male subordination was a paternal investment (Pollock, 1979).

The structures of prosimian and simian troops are amazingly alike in regard to interindividual relationship and the intersexual hierarchy. The main difference is the lemur female dominance. In simians, males are dominant with feeding priority. This male dominance, including that observed in humans, could be problematic in that female feeding priority might improve the diet quality during lactation period, which could in turn be advantageous for reproduction.

However, our results comparing the most and the least dominant females' energy expenditure during each reproduction period seems to assert the absence

of correlation between the three parameters of dominance within sexes, dominance between sexes, and energy expenditure.

Thus, the systems involving female or male dominance or males may result mainly from a remnant of the evolution history of prosimians and simians, respectively, even though both systems are efficient and contribute to the animals' adaptability.

The example cited at the beginning of the "Discussion" section shows an example of apparent mutual aid between next of kin individuals of the troop. Jolly (1999) argued that among evolutionary mechanisms, cooperation as much as competition has progressively modeled the life forms on the planet Earth. This idea keeps recurring, although it is relatively recent, in interpreting selection pressures (Leigh, 1999). Neither sexual selection nor individual competition is sufficient to explain group structures for which one should actually take much more account of kin selection. Genes responsible for subordination behavior might be selected because such behavior might raise the reproductive possibilities of kin and dominant individuals.

Although social behavior is not directly linked to energy expenditure, we could conclude that adaptation mechanisms to energetic resources are based on the troop relationship with its environment, but that this relationship is more complex than simple dominance hypotheses can explain.

*Acknowledgments.* We are grateful to Marcel Hladik, Patrick Pasquet, Bruno Simmen, and Alison Jolly who recognized the difficulty of comparing social behavior with physiological state and gave very helpful and relevant advice to improve this work. We also thank the de Heaulme family for permission to conduct the study in their reserve. This research received support from WWF-US Russell E. Train Educational for Nature.

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