



**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2007

Female Social Dominance in Two Eulemur Species With Different Social Organizations

Marolf, B ; McElligott, A G ; Müller, A E

DOI: <https://doi.org/10.1002/zoo.20135>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-257>

Journal Article

Accepted Version

Originally published at:

Marolf, B; McElligott, A G; Müller, A E (2007). Female Social Dominance in Two Eulemur Species With Different Social Organizations. *Zoo Biology*, 26(3):201-214.

DOI: <https://doi.org/10.1002/zoo.20135>

Female social dominance in two *Eulemur* species with different social organizations

Brigitte Marolf¹, Alan G. McElligott², Alexandra E. Müller¹

¹*Anthropologisches Institut und Museum, Universität Zürich, Switzerland*

²*Zoologisches Institut, Universität Zürich, Switzerland*

Short title: Female social dominance in *Eulemur*

Correspondence and current address:

Alan McElligott, School of Biology, Biology Building, University of Nottingham, University Park, Nottingham NG7 2RD, UK.

Tel + 44 115 9513231

Fax + 44 115 9513251

Email amcellig1@yahoo.ie

Abstract

Female social dominance is rare in mammals, but common in lemurs. We investigated social dominance in two *Eulemur* species; the polygynous crowned lemur (*E. coronatus*) and the monogamous red-bellied lemur (*E. rubriventer*), using four and two social groups, respectively. We collected data on agonistic interactions and two types of affiliative behavior (grooming and maintaining spatial proximity). We used a combination of focal watches of individuals, instantaneous scan-sampling of groups, and all-occurrence of some behaviors in groups. We found that overall rates of agonistic interactions were higher in *E. coronatus*, and they also had more decided intersexual agonistic interactions than *E. rubriventer*. However, in both species the females won the vast majority of these agonistic interactions. *E. coronatus* females were groomed more often by males than *vice versa*, whereas no sex differences in grooming were observed in *E. rubriventer*. We found that males were responsible for maintaining spatial proximity in *E. coronatus* whereas in *E. rubriventer*, females were responsible. In one group of *E. coronatus*, the male was overweight and dominant to the female and this is the first observation of male dominance in a lemur species typically described as female dominant. We suggest that body weights in captivity be monitored for maintaining normal dominance relationships. Overall, agonistic behaviors were consistent with clear female social dominance in both *E. coronatus* and *E. rubriventer*. The affiliative behaviors also provided clear evidence for female dominance *E. coronatus*, but not for *E. rubriventer*.

Key words: agonistic interaction; grooming; *Eulemur coronatus*; *Eulemur rubriventer*; monogamy; polygyny

INTRODUCTION

Dominance has been used to indicate priority of access to food, water and partners, as well as superiority in agonistic interactions [Ellis, 1995]. In mammals, males are usually the dominant sex as they compete for receptive females. This has resulted in sex differences in body size, fighting abilities and morphological characteristics such as canines, horns and antlers that contribute to asymmetries in agonistic power during intersexual conflicts [Crook and Gartlan, 1966; Clutton-Brock and Harvey, 1977; Smuts, 1987; Plavcan and van Schaik, 1992; McElligott et al., 2001; Saunders et al., 2005].

Female social dominance exists when females consistently win most agonistic interactions and also cause submissive behavior in males [Pereira et al., 1990]. While uncommon among mammals, it is found in spotted hyenas (*Crocuta crocuta*) and is common among lemurs [Frank, 1986; Kappeler, 1993; Dloniak et al., 2006]. Lemurs do not show dimorphism in body or canine size, and this indicates that the intensity of intrasexual selection is comparatively low. The lack of dimorphism has also been suggested as an important prerequisite for female dominance in lemurs [Kappeler, 1993].

Female social precedence among lemurs has been referred to both as female dominance [Richard, 1987], and as female feeding priority [Jolly, 1984]. These different concepts allow for different proximate behavioral mechanisms. Female dominance can only be attained through agonistic superiority, whereas female feeding priority could be brought about by males, in which case the best description would be “male deference” [Hrdy, 1981, Kappeler, 1993]. Moreover, feeding priority implies only consistent priority of access to food, and not necessarily to other resources [Hand, 1986].

There are varying forms of female social dominance relationships within lemur species and these depend on the proportion of agonistic interactions that females win against males. Some species are more clearly female dominant than others and there is a continuum in between [Pollock, 1979; Jolly, 1984; Kappeler, 1989; Pereira et al., 1990; Rendall, 1993; Meyer et al., 1999; Radespiel and Zimmermann, 2001; Digby and Kahlenberg, 2002; Richard, 2003; Schülke

and Kappeler, 2003; Waeber and Hemelrijk, 2003; Overdorff et al., 2005]. Female social dominance is thought to be absent in red-fronted lemurs [*Eulemur fulvus rufus*; Pereira et al., 1990; Pereira and McGlynn 1997; Ostner and Kappeler, 1999; Sussman 1999]. Nevertheless, complete male dominance, which is typical for polygynous mammals, has not been reported for any lemur species.

To date, the evolutionary significance of female dominance is not fully understood and two main hypotheses have been postulated to explain its existence. Hrdy [1981] proposed the male deference hypothesis, which suggests that females have feeding priority when males do not need higher-quality food, and therefore males can defer to females and/or when breeding is seasonal. The reproductive stress hypothesis by Jolly [1984] proposes that females should dominate males when ecological variables and metabolic factors challenge female reproductive success.

Erhart et al. [2002] stated that female dominance measured using the outcomes of agonistic interactions among prosimians is more pronounced in captive than in wild groups, and as a result, agonistic interactions alone might not be the best indicator of female dominance. Therefore in addition to intersexual agonistic interactions and submissive behaviors, we studied the following affiliative behaviors: grooming and maintaining spatial proximity. The affiliative behaviors can be used alongside the results of the other interactions to evaluate in greater detail female social dominance [Kubzdela et al., 1992; Radespiel and Zimmermann, 2001; Manson et al., 2004; Singh et al., 2006]. We used two closely related lemurid species with different social organizations; the polygynous crowned lemur (*E. coronatus*) and the monogamous red-bellied lemur (*E. rubriventer*). In polygynous species intragroup competition for mate partners is intense, and studies in captivity have shown that *E. coronatus* females are dominant to males [Kappeler, 1989; Pereira et al., 1990]. By contrast, most aggression in monogamous groups is directed toward outsiders of the same sex and rare between mates. Therefore the expression of female dominance might be weaker and species such as *E. rubriventer* are considered not to be female dominant [Pollock, 1979; Hrdy, 1981; Curtis and Zaramody, 1999]. Rates of agonistic

and other social interactions may vary seasonally depending on when breeding occurs, and as a result it is also important to examine this factor. The aim of this study was therefore to investigate whether the difference in social organization influences the agonistic and affiliative behaviors, and hence female dominance patterns.

METHODS

Animals and housing conditions

This study was carried out on four groups of *E. coronatus* (denoted c1, c2, c3 and c4) and two groups of *E. rubriventer* (denoted r1 and r2) in the Parc Zoologique et Botanique, Mulhouse, France (Table 1). All groups were kept in indoor cages (size: 1.8-5 m²) and had access to outdoor runs (average size: 16m²), which were visible for zoo visitors. The c1 group occupied their own cage and c2 was housed with two female *Hapalemur griseus occidentalis*. Two groups of *E. coronatus* (c3, c4) shared one outdoor cage; one group in the morning and the second group in the afternoon. Similarly, the two groups of *E. rubriventer* (r1, r2) shared an outdoor cage; one group each in the morning and afternoon. All lemurs were fed once per day with a combination of milky bread and a variety of fruits and vegetables; water was provided *ad libitum*.

<- Table 1

Data collection

Observations took place between September 2002 and May 2003 for a total of 156 hr (range: 20.5-35 hr/group). Data were collected before and during the breeding season as well as during the birth season. The breeding season was defined as the time from the first signs of sexual interest until the estimated fertilization (c1, c2 and c4, mid November until end of January; c3 and r2, mid November until end of December; r1, mid November until end of May). Births only occurred in c3 and r2 and therefore the remaining observations for these two groups were additionally divided into gestation and birth seasons (births took place on April 29 in c3 and April 4 in r2). All adult group members (age >20 months at the beginning of the study) served as focal animals. Every individual was selected randomly for a 30-min focal watch, and each was observed at least once per week. Observations were conducted from 08:00 until 18:00. The behavior of all adult individuals in a group was collected instantaneously at 1-min intervals [Altmann, 1974].

We recorded all instances of agonistic and affiliative interactions between group members as well as the initiators and receivers of any interactions. We distinguished between decided and undecided interactions (*sensu* Pereira et al., 1990], in relation to agonistic interactions. Decided interactions are when one animal shows aggressive and the other submissive behavior (A-S), or when one animal shows spontaneous submissive behavior without any aggression from the opponent (0-S). The activity of the focal animal was recorded before and after the agonistic interaction, in order to define the behavioral context of each interaction. These contexts were defined as follows: feeding (one or both members of a dyad at the feeding place prior to agonistic interaction); social (both members of a dyad in non-agonistic physical contact prior to agonistic interaction); sexual (attempted or successful copulation prior to agonistic interaction); spatial (none of the other contexts).

Data analysis

We compared the total amount of decided agonistic interactions won and which sex was groomed more by the other, to determine if the females were the dominant sex. A χ^2 -test was used to evaluate 1) the outcome of all decided intersexual aggressive interactions against the hypothesis that females were as likely to win as males and 2) the initiation of grooming bouts per dyad against the hypothesis that females initiated grooming as often as males. Additionally, these findings were compared with the dominance index of Zumpe and Michael [1986]. This is a commonly used method, which is based on the direction of aggressive interactions between all possible pairs in a social group, can be used when fights have not occurred, and is independent of agonistic interaction frequency [Zumpe and Michael, 1986; Bayly et al., 2006]. Mann-Whitney *U*-tests and Kruskal-Wallis-tests were used to compare the mean agonistic rate/hr in different seasons, and the Nemenyi-test was used for multiple comparisons [Zar, 1999]. All tests are 2-tailed and factors were considered to have a statistically significant influence if $P < 0.05$. Descriptive statistics were reported as means and standard deviation.

We used the Hinde-Index [Hinde and Atkinson, 1970] to determine which individual of a dyad was responsible for maintaining spatial proximity between pair partners in affiliative contexts. We measured the extent to which individual A is responsible for maintaining proximity between itself and individual B as follows:

$$\text{A's responsibility for proximity} = \frac{U_A}{U_A + U_B} - \frac{S_A}{S_A + S_B}$$

where U_A =number of occasions when the pair was united by A's movements; U_B = number of occasions when the pair was united by B's movements; S_A =number of occasions when the pair was separated by A's movements; and S_B = number of occasions when the pair was separated by B's movements. The index ranges from -1 (B totally responsible for maintaining proximity) to $+1$ (A totally responsible for maintaining proximity). A value of 0 indicates that A and B were equally responsible for maintaining proximity.

RESULTS

Intersexual agonistic interactions

Overall, intersexual agonistic interactions occurred 3.6 ± 1.7 times/hr in *E. coronatus* and 1.4 ± 1.1 times/hr in *E. rubriventer*. In *E. coronatus*, 83.0% (352/424) of agonistic interactions between male and female were decided, and in *E. rubriventer* the proportion of decided agonistic interactions was 53.1% (34/64). *E. coronatus* and *E. rubriventer* females won the vast majority of decided agonistic interactions: 88.1% (310/352) and 88.2% (30/34), respectively (Table 2). In 42.1% (148/352) of *E. coronatus* decided agonistic interactions, one of the sexes showed spontaneous submissive behavior. *E. coronatus* females caused much more submissive behavior from males than *vice versa* (137 compared to 11 cases, respectively). In *E. rubriventer*, males showed 8 spontaneous submissions towards females, and females did not show any spontaneous submissions.

At group level, females won significantly more decided agonistic interactions than males in three of the four *E. coronatus* groups (c2, c3, c4) and in one *E. rubriventer* group (r1), (Table 2). In one *E. coronatus* group (c1), the male won significantly more interactions than the female. In the second *E. rubriventer* group (r2), there was a trend that the female won more agonistic interactions (Table 2). In groups containing adult offspring (c3, r1) there were no differences in the results of agonistic interaction between parent-offspring dyads. However, after giving birth, the mother in c3 became highly aggressive towards the oldest daughter in the group (Table 2). There were no agonistic interactions between this pair during the other seasons (B. Marolf, unpublished data).

<– Table 2

In three of the four *E. coronatus* groups (c1, c2, c4), the agonistic interaction rate was low and did not differ between the non-breeding and the breeding season (Mann-Whitney *U*-test, c1: $n_{nb}=17$, $n_{br}=12$, $U=95.5$, ns; c2: $n_{nb}=12$, $n_{br}=17$, $U=97.0$, ns; c4: $n_{nb}=19$, $n_{br}=12$, $U=103.5$, ns; Fig. 1). The c3 group was the only one in which a birth occurred; aggression rates were highest during the non-breeding season and decreased afterwards during breeding season, gestation and

birth season (Kruskal-Wallis test, $n_{nb}=7$, $n_{br}=9$, $n_g=13$, $n_b=7$, $H=14.72$, $P=0.002$; Fig. 1). The intersexual agonistic interaction rate differed between non-breeding and birth season, non-breeding season and gestation, and between the breeding season and birth season (Nemenyi-test, $Q \geq 3.02$, $P < 0.05$). The intersexual agonistic interaction rate did not differ between the non-breeding and gestation season, the non-breeding and birth season or between the gestation and birth season.

<- Figure 1

In one *E. rubriventer* group (r1), the agonistic interaction rate increased significantly during the breeding season compared to the non-breeding season (Mann-Whitney *U*-test, $n_{nb}=6$, $n_b=15$, $U=18.5$, $P=0.03$; Fig. 2). This high agonistic rate was mostly in the sexual context and only seen around estrus, when the males tried to mount the female and she rejected them (B. Marolf, personal observation). In r2, no aggression was observed during the non-breeding season and the agonistic rate did not differ between seasons (Kruskal-Wallis-test: $n_{nb}=6$, $n_{br}=7$, $n_p=10$, $n_b=9$, $H=6.91$, ns; Fig. 2).

<- Figure 2

Agonistic interactions occurred during feeding and non-feeding contexts (Fig. 3). In *E. coronatus*, 48% of all agonistic interactions occurred during feeding but there were differences at the group level. In two groups the majority of agonistic interactions occurred during the feeding context (c1, 94.2%; c3, 58.2%), whereas in the other groups the proportion of agonistic interactions taking place during feeding was comparatively low (c2, 9.5%; c4, 27.7%). In c2, 67.6% of agonistic interactions occurred in the spatial context when the male spontaneously deferred to the female when she approached the preferred resting place. In c4, the agonistic interactions were evenly distributed in the different contexts (Fig. 3).

In *E. rubriventer*, agonistic interactions were most common in the social context (r1: 38.3%; r2: 58.8%; Fig. 3). In r1, 38.3% of all agonistic interactions occurred in the sexual context and these only occurred around days of copulation, whereas such agonistic interactions were never observed in r2. Compared to *E. coronatus*, agonistic interactions during feeding time were rare (r1, 6.4%; r2, 11.8%).

<- Figure 3

Affiliative behavior

In *E. coronatus*, three out of four adult males initiated significantly more grooming than females (Table 3). Only the female of c1 groomed the male significantly more often than *vice versa*. In c3, the adult daughter initiated significantly more grooming bouts towards her parents than vice versa. In *E. rubriventer*, no difference in initiating grooming bouts between the sexes was found (Table 3). In r1, the adult son groomed his father more often whereas there was no difference between him and his mother.

In all *E. coronatus* groups, the male was responsible for maintaining proximity, whereas in *E. rubriventer*, the females were responsible (Table 3). In both groups with adult offspring (c3 and r1), the adult offspring maintained the proximity with their parents (Table 3).

<- Table 3

Social dominance

We calculated the rank order using 1) the outcome of decided agonistic interactions, 2) grooming and 3) the dominance index of Zumpe and Michael [1986], (Table 4). In two *E. coronatus* groups (c2, c4), the females dominated the males. In c3, the adult female was clearly dominant to the adult male, whereas the rank of the adult daughter was unclear. The dominance index of Zumpe and Michael [1986] showed that she dominated her father, whereas no difference in the outcome of decided agonistic interactions was found. Furthermore, she initiated more grooming bouts toward her father than he initiated towards her. In c1 the male was dominant to the female (Table 4). In the *E. rubriventer* groups, the females dominated the males in agonistic interactions, but the initiation of grooming bouts did not differ (Table 4).

<- Table 4

DISCUSSION

We examined agonistic and affiliative behaviors in relation to female social dominance in polygynous *E. coronatus* and monogamous *E. rubriventer*. Both species were kept as family groups, although wild *E. coronatus* live in multi male-multi female groups. We found evidence for female dominance in both species, but there were differences in how this dominance was expressed. *E. coronatus* had higher rates of intersexual aggression than *E. rubriventer* and more than 80% of *E. coronatus* agonistic interactions were decided. By contrast, only half of *E. rubriventer* agonistic interactions were decided. However, in both *E. coronatus* and *E. rubriventer*, the vast majority of decided agonistic interactions were won by females. Grooming behavior provided additional evidence for female dominance in *E. coronatus*, but not for *E. rubriventer*. In three of the four *E. coronatus* groups, males initiated more grooming, whereas there were no sex differences in grooming for *E. rubriventer*. In *E. coronatus*, males were responsible for maintaining proximity, whereas females maintained proximity in *E. rubriventer*. We suggest that the different social organizations of these two closely related *Eulemur* species, is one of the main reasons for the differences in aggressive and affiliative behaviors.

Most studies of lemurs indicate that aggression occurs mostly during feeding. Therefore, it has been proposed that female feeding priority is part of a behavioral strategy to maximize foraging efficiency, particularly during gestation and lactation [Jolly, 1984; Richard, 1987]. The agonistic interaction rate that we found in *E. coronatus* is similar to that found by Kappeler [1989] but higher than in the wild [Freed, 1996]. Wild *E. coronatus* often split into subgroups and feed and rest alone [Freed, 1996]. This may explain the higher aggression rate that we found in captive animals, because they are forced to be closer. A similar effect has been shown in captive gorillas (*Gorilla gorilla*) where the aggression rate was higher in an indoor cage than in a larger outdoor cage [Hoff et al., 1997]. As in Verreaux' sifakas (*Propithecus verreauxi verreauxi*) where feeding competition increases with the number of animals in the group [Kubzdela, 1997], we found the highest agonistic rate in the largest *E. coronatus* lemur group. The rate of agonistic interaction decreased only in the *E. coronatus* group that bred successfully.

This is similar to the findings of Kappeler [1989], who showed that the rate of agonistic interactions between males and females tended to decrease in the breeding season, and that males in non-breeding pairs were more aggressive toward their mates than in pairs in which breeding occurred.

In *E. rubriventer*, agonistic interactions differed between the groups and seasons. In the group containing an adult son (r1), the agonistic interaction rate was two times higher than in r2. The agonistic interaction rate also increased in r1 during the breeding time, whereas there was no seasonal difference in r2. However, most aggression was limited to the few days around estrous when both males tried to mount the female (B. Marolf, personal observation). Therefore the increased aggression seen in this group may have been an artifact of their captivity, because in the wild an adult pair would not be accompanied an adult male son. The females won most agonistic interactions against the males and could also evoke more submissive behaviors. In two other monogamous lemur species that have been studied in detail, the mongoose lemurs (*Eulemur mongoz*) and indris (*Indri indri*), females dominate the males and have priority of access to food [Pollock, 1979; Curtis and Zaramody, 1999; Powzyk, 1997]. In contrast to these two species in which most agonistic interactions occurred during feeding, agonistic interactions between *E. rubriventer* in our study mostly occurred in other contexts. However, food was widely scattered throughout the cage and this probably reduced the occurrence of agonistic interactions during feeding.

In *E. coronatus*, most agonistic interactions were won by females and in one third of all agonistic interactions, females won without showing any aggressive behavior. This is in contrast to Pereira et al. [1990], in which males only expressed submission after they were aggressively attacked by females. In the wild, females evoked submissive behaviors from males in half of all female-initiated agonistic interactions, whereas this was the case for males in less than 10% [Freed, 1996].

In contrast to other captive studies [Kappeler, 1989; Pereira et al., 1990], the male in one *E. coronatus* group (c1) was dominant to the female. In c1, the male was much larger than the

female and this may have been responsible for his dominance. Following our study, the food given to the male was reduced, he lost weight and the female became more aggressive [De Michelis, pers. comm.]. This suggests that obesity of captive lemurs [Terranova and Coffman, 1997], can influence the normal functioning of dominance relationships.

Differences in grooming between sexes are known from prosimians and can be used as an indication of social dominance [Richard and Heimbuch, 1975; Manson et al., 2004; Singh et al., 2006]. In *E. coronatus*, we found that females were generally groomed more often by males, than males were groomed by females. However, we observed two exceptions. First, in one group (c1) the male was groomed more often by the female and the male also dominated the female. Second, in another group (c3) the adult daughter initiated more grooming bouts toward her father, than the father towards its daughter. In *E. rubriventer*, we found no sex differences in grooming. In another monogamous species, male indris groomed females more often than females groomed males [Pollock, 1979]. These results indicate that the relationship between female dominance and grooming behavior in lemurs is not always straightforward [Kappeler, 1989; Pereira et al., 1990].

We found that male *E. coronatus* were responsible for maintaining spatial proximity whereas in *E. rubriventer*, females were responsible. We expected male *E. rubriventer* to be responsible for maintaining proximity because in monogamous species infant-carrying is advantageous for male fitness, and proximity maintenance and infant-carrying are linked [Pollock, 1979]. Our findings also differ from studies of another monogamous species, the mongoose lemur, in which males seek contact with their females [Curtis and Zaramody, 1999]. One reason for this difference might be that in *E. rubriventer*, males carry their infants for a substantial amount of time while male mongoose lemurs only carry their infants for very short periods [Overdorff, 1988; Curtis and Zaramody, 1999]. *E. rubriventer* females might therefore be more dependent on their mates than other monogamous lemurs.

In conclusion, we found evidence for female dominance in both *E. coronatus* and *E. rubriventer*. In polygynous *E. coronatus*, all the agonistic and affiliative behaviors that we

measured were indicative of female dominance. However the evidence for monogamous *E. rubriventer* was less clear, with agonistic behaviors indicating female dominance, and some affiliative behaviors not signifying female dominance. *E. coronatus* live in multi male/multi female groups with high levels of agonistic activity, and females mate with more than one male [Kappeler, 1989; Pereira et al., 1990; Freed, 1996]. If females are more likely to mate with males which defer to them and stay close, then the subordinate behaviors of *E. coronatus* males might be a strategy to increase their own fitness. For example, red-fronted brown lemur (*Eulemur fulvus rufus*) males gain long-term reproductive success by assisting females while feeding [Overdorff, 1998]. By contrast, *E. rubriventer* pairs have much lower levels of agonistic interactions and certainty of paternity is higher, resulting in less marked female dominance. To verify female dominance in *E. coronatus* and *E. rubriventer*, further research should be conducted in the wild

CONCLUSIONS

1. Three out of four *E. coronatus* groups and both *E. rubriventer* groups exhibited agonistic behaviors consistent with female dominance. Females won significantly more interactions than males and they could also evoke more submissive behaviors from males.
2. There was evidence for female dominance from the affiliative behaviors in *E. coronatus*, but not *E. rubriventer*.
3. In one *E. coronatus* group the male was dominant but this probably resulted from the male being overweight. We suggest that body weights in captivity be monitored in order to protect the normal functioning of dominance relationships.

ACKNOWLEDGEMENTS

We thank Drs. Pierre Moisson and Jean-Marc Lernoould of the Parc Zoologique de Mulhouse for giving permission to conduct this study. Very special thanks go to the animal keepers and Sara de Michelis for help and for providing us with information on the animals, and we are grateful to the reviewers for their comments on the manuscript. This project was financed by the A.H. Schultz Foundation and the Schweizerische Gesellschaft für Anthropologie.

REFERENCES

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-256.
- Bayly KI, Evans CS, Taylor T. 2006. Measuring social structure: a comparison of eight dominance indices. *Behav Proc* 73:1-12.
- Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organisation. *J Zool* 183:1-39.
- Crook JH, Gartlan JS. 1966. Evolution of primate societies. *Nature* 210:1200-1203.
- Curtis DJ, Zaramody A. 1999. Social structure and seasonal variation in the behaviour of *Eulemur mongoz*. *Folia Primatol* 70:79-96.
- Digby LJ, Kahlenberg SM. 2002. Female dominance in blue-eyed black lemurs (*Eulemur macaco flavifrons*). *Primates* 43:191-199.
- Dloniak SM, French JA, Holekamp KE. 2006. Rank-related maternal effects of androgens on behaviour in wild spotted hyaenas. *Nature* 440, 1190-1193
- Ellis L. 1995. Dominance and reproductive success among non-human animals: a cross-species comparison. *Ethol Sociobiol* 16:257 - 333.
- Erhart E, Overdorff D, Mutschler T. 2002. Rates of agonism by lemurid primates: Implication for establishing female dominance. *Am J Phys Anthropol* 34:67.
- Frank LG. 1986. Social organisation of the spotted hyena (*Crocuta crocuta*). II. Dominance and reproduction. *Anim Behav* 35:1510-1527.

- Freed BZ. 1996. Co-occurrence among crowned lemurs (*Lemur coronatus*) and Sanford's lemurs (*Lemur fulvus sanfordi*) of Madagascar. (dissertation). St. Louis: Washington University.
- Hand JL. 1986. Resolution of social conflicts: egalitarianism, spheres of dominance and game theory. *Q Rev Biol* 61:201-220.
- Hinde RA, Atkinson S. 1970. Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. *Anim Behav* 18:169-176.
- Hoff MP, Powell DM, Lukas KE, Maple TL. 1997. Individual and social behavior of lowland gorillas in outdoor exhibits compared with indoor holding areas. *Appl Anim Behav Sci* 54:359-370.
- Hrdy SB. 1981. *The woman that never evolved*. Cambridge: Harvard University Press.
- Jolly A. 1984. The puzzle of female feeding priority. In: Small MF, editor. *Female primates studies by woman primatologists*. New York: Alan R Liss. p 197-215.
- Kappeler PM. 1989. Agonistic and grooming behavior of captive crowned lemurs (*Lemur coronatus*) during the breeding season. *Hum Evol* 4:207-215.
- Kappeler PM. 1993. Female dominance in primates and other mammals. In Bateson PPG, Klopfer PH, Thompson NS, editors. *Perspectives in ethology vol. 10: behavior and evolution*. New York: Plenum Press. p 143-158.
- Kubzdela KS. 1997. Sociodemography in diurnal primates: the effects of group size and female dominance rank on intra-group spatial distribution, feeding competition, female reproductive success, and female dispersal patterns in white sifakas, *Propithecus verreauxi verreauxi*. (dissertation). Chicago: University of Chicago.
- Kubzdela KS, Richard AF, Pereira ME. 1992. Social relations in semi-free-ranging sifakas (*Propithecus verreauxi coquereli*) and the question of female dominance. *Am J Primatol* 28:139-145

- Manson JH, Navarette CD, Silk JB, Perry S. 2004. Time-matched grooming in female primates? New analyses from two species. *Anim Behav* 67:493-500.
- McElligott AG, Gammell MP, Harty HC, Paini DR, Murphy DT, Walsh JT, Hayden TJ. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behav Ecol Sociobiol* 49:266-272.
- Meyer C, Gallo T, Schultz ST. 1999. Female dominance in captive red ruffed lemurs, *Varecia variegata* (Primates, Lemuridae). *Folia Primatol* 70:358-361.
- Ostner J, Kappeler PM. 1999. Central males instead of multiple pairs in redfronted lemurs, *Eulemur fulvus rufus* (Primates, Lemuridae)? *Anim Behav* 58:1069-1078.
- Overdorff DJ. 1988. Preliminary report on the activity cycle and diet of the red-bellied lemur (*Lemur rubriventer*) in Madagascar. *Am J Primatol* 16:143-153.
- Overdorff DJ. 1998. Are *Eulemur* species par-bonded? Social organization and mating strategies in *Eulemur fulvus rufus* from 1988-1995 in Southeast Madagascar. *Am J Phys Anthropol* 105:153-166.
- Overdorff DJ, Erhart EM, Mutschler T. 2005. Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (*Varecia variegata*) in southeastern Madagascar? *Am J Primatol* 66:7-22.
- Pereira ME, McGlynn CA. 1997. Special relationships instead of female dominance for redfronted lemurs, *Eulemur fulvus fulvus*. *Am J Primatol* 43:239-258.
- Pereira ME, Kaufmann R, Kappeler PM, Overdorff DJ. 1990. Female dominance does not characterize all of the Lemuridae. *Folia Primatol* 55:96-103.
- Plavcan JM, van Schaik CP. 1992. Intrasexual competition and canine dimorphism in anthropoid primates. *Am J Phys Anthropol* 87:461-477.
- Pollock JJ. 1979. Female dominance in *Indri indri*. *Folia Primatol* 31:143-164.
- Powzyk JA. 1997. The socio-ecology of two sympatric indrids: *Propithecus diadema diadema* and *Indri indri*, a comparison of feeding strategies and their possible repercussions on species-specific behaviors. (dissertation). Durham: Duke University.

- Radespiel U, Zimmermann E. 2001. Female dominance in captive mouse lemurs (*Microcebus murinus*). *Am J Primatol* 54:181-192.
- Rendall D. 1993. Does female social precedence characterize captive aye-ayes (*Daubentonia madagascariensis*)? *Folia Primatol* 14:125-130.
- Richard AF. 1987. Malagasy prosimians: female dominance. In Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 25-33.
- Richard AF. 2003. *Propithecus*, sifakas. In Goodman SM, Benstead JP, editors. *The natural history of Madagascar*. Chicago: University of Chicago Press. p 1345-1348.
- Richard AF, Heimbruch R. 1975. An analysis of the social behavior of three groups *Propithecus verreauxi*. In Tattersall J, Sussmann RW, editors. *Lemur biology*. New York: Plenum Press. p 313-333.
- Schülke O, Kappeler PM. 2003. So near and yet so far: territorial pairs but low cohesion between pair partners in a nocturnal lemur, *Phaner furcifer*. *Anim Behav* 65:331-343.
- Saunders FC, McElligott AG, Safi K, Hayden TJ. 2005. Mating tactics of male feral goats (*Capra hircus*): risks and benefits. *Acta Ethol* 8:103-110.
- Singh M, Krishna BA, Singh M. 2006. Dominance hierarchy and social grooming in female lion-tailed macaques (*Macaca silenus*) in the Western Ghats, India. *J Biosci* 31:369-377.
- Smuts BB. 1987. Sexual competition and mate choice. In Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 385-399.
- Sussman RW. 1999. *Primate ecology and social structure, vol. 1: lorises, lemurs and tarsiers*. Needham Heights: Pearson Custom Publishing.
- Terranova CJ, Coffmann BS. 1997. Body weights of wild and captive lemurs. *Zoo Biol* 16:17-30.
- Waeber PO, Hemelrijk CK. 2003. Female dominance and social structure in Alaotran gentle lemurs. *Behaviour* 140:1235-1246.

Zar JH. 1999. Biostatistical analysis, 4th ed. Englewood Cliffs: Prentice Hall.

Zumpe D, Michael RP. 1986. Dominance index: a simple measure of relative dominance status in primates. *Am J Primatol* 10:291-300.

TABLE 1. Demographic data of *E. coronatus* (c1 to c4) and *E. rubriventer* (r1 and r2) groups. The breeding pair of each group is listed first. Z = studbook number; ? = unknown; + = wild born; - = captive born.

Species	Group	Animal	Z	Sex	Birth date	Wild		
						born	Father	Mother
<i>E. coronatus</i>	c1	Eloi	920035	M	?	+	?	?
		Pia	990211	F	18.07.1999	-	920036	880050
		Tina	M02055	F	19.05.2002	-	Eloi	Pia
	c2	Serapis	910106	M	14.04.1981	-	?	?
		Nicole	970118	F	22.05.1997	-	Eloi	920038
	c3*	Felix	930034	M	30.04.1993	-	Eloi	920038
		Julie	940070	F	07.04.1994	-	920036	880050
		Pauline	990076	F	20.04.1999	-	Felix	Julie
		Talata	M02027	F	13.04.2002	-	Felix	Julie
		Ugo	M03051	M	29.04.2003	-	Felix	Julie
	c4	Rak	M-0054	M	22.04.2000	-	Felix	Julie
		Rosalie	M01045	F	2000	+ ¹⁾	?	?
		Tango	M022057	M	22.05.2002	-	Rak	Rosalie
<i>E. rubriventer</i>	r1	Bebe	860003	M	1983 ²⁾	+	?	?
		Jody	940045	F	21.04.1994	-	Sandy	Diane
		Poly ³⁾	990067	M	14.04.1999	-	Bebe	Jody
		Ursula	M03127	F	04.09.2003	-	Bebe	Jody

r2*	Sandy	910121	M	21.06.1989	-	?	?
	Diane	910020	F	?	+	?	?
	Sara	M01020	F	03.04.2001	-	Sandy	Diane
	Tovo	M02082	M	24.05.2002	-	Sandy	Diane
	Urrikan	M03034	M	04.04.2003	-	Sandy	Diane

¹⁾ Confiscated

²⁾ Wild caught 1986 and thought to be aged 3 years.

³⁾ Taken out of group in February 2003

* Breeding occurred during study. Note that the birth in r1 occurred very late in the year.

TABLE 2. Rate of agonistic interactions per hour, absolute number of agonistic interactions, and decided agonistic interactions throughout the observation period for each adult dyad per group (*E. coronatus*, c1 to c4; *E. rubriventer*, r1 and r2). F=females, M=males.

Group	Dyad	Sex	Rate of agonistic interactions/hr	Absolute number of agonistic interactions	Decided agonistic interactions	χ^2	<i>P</i>
c1	Pia-Eloi	F-M	0.75 - 1.29	19 - 33	13 - 30	5.90	0.02
c2	Nicole-Serapis	F-M	2.48 - 0.56	62 - 14	53 - 8	31.77	<0.001
c3	Julie-Felix	F-M	5.24 - 0.00	186 - 0	176 - 0	1.74	<0.001
	Pauline-Felix	F-M	0.48 - 0.28	17 - 10	8 - 3	1.45	0.13
	Julie-Pauline	F-F	1.18 - 0.00	42 - 0	36 - 0	34.03	<0.001
c4	Rosalie-Rak	F-M	3.31 - 0.08	81 - 2	60 - 1	55.15	<0.001
r1	Jody-Bebe	F-M	1.35 - 0.22	31 - 5	19 - 2	12.19	<0.001
	Jody-Poly ‡	F-M	0.34 - 0.20	7 - 4	4 - 1	0.80	0.18
	Bebe-Poly ‡	M-M	0.20 - 0.10	4 - 2	2 - 0	0.50	0.32
r2	Diane-Sandy	F-M	0.85 - 0.15	14 - 3	7 - 1	3.13	0.08

‡ taken out of group in February 2003

TABLE 3. Mean number of grooming bouts per hour and the absolute number of grooming bouts throughout the observation period for each adult dyad (*E. coronatus*, c1 to c4; *E. rubriventer*, r1 and r2). F = female, M = male.

Group	Dyad	Sex	Mean grooming bouts/hr	Absolute amount of grooming	χ^2	<i>P</i>	Hinde index
c1	Pia-Eloi	F-M	0.63 - 0.20	16 - 5	4.76	0.03	-0.28
c2	Nicole-Serapis	F-M	0.36 - 1.20	9 - 30	10.26	<0.001	-0.31
c3	Julie-Felix	F-M	0.01 - 0.82	2 - 29	21.81	<0.001	-0.33
	Pauline-Felix	F-M	1.53 - 0.48	39 - 17	7.88	0.005	0.29
	Julie-Pauline	F-F	0.00 - 1.21	0 - 43	41.02	<0.001	-0.65
c4	Rosalie-Rak	F-M	0.49 - 1.59	12 - 39	13.25	<0.001	-0.33
r1	Jody-Bebe	F-M	0.43 - 0.30	10 - 7	0.24	0.47	0.39
	Jody-Poly*	F-M	0.20 - 0.29	4 - 6	0.10	0.53	-0.57
	Bebe-Poly*	M-M	0.15 - 0.83	3 - 17	8.45	0.004	-0.36
r2	Diane-Sandy	F-M	1.90 - 1.60	38 - 32	0.36	0.47	0.02

¹⁾ The χ^2 value and the probability (*P*) that both animals per dyad groom the other as often as it gets groomed are given.

²⁾ The Hinde-index indicates which individual is responsible for maintaining spatial proximity. Values below 0 indicate that the second animal in a dyad is responsible.

TABLE 4. Comparison of rank order per group (*E. coronatus*, c1 to c4; *E. rubriventer*, r1 and r2). The rank order was determined using decided agonistic interactions, grooming and the dominance index of Zumpe and Michael [1986].

Group	Female	Male	Offspring
Group c1	Pia	Eloi	
Rank order determined with decided agonistic interactions	2	1	
Rank order determined with grooming	2	1	
Dominance index [Zumpe and Michael 1986]	29.05	70.5	
Group c2	Nicole	Serapis	
Rank order determined with decided agonistic interactions	1	2	
Rank order determined with grooming	1	2	
Dominance index [Zumpe and Michael 1986]	83.20	16.80	
Group c3	Julie	Felix	Pauline
Rank order determined with decided agonistic interactions	1	2.5	2.5
Rank order determined with grooming	1	2	3
Dominance index [Zumpe and Michael 1986]	98.45	18.38	31.38
Group c4	Rosalie	Rak	
Rank order determined with decided agonistic interactions	1	2	
Rank order determined with grooming	1	2	
Dominance index [Zumpe and Michael 1986]	88.40	11.60	
Group r1	Jody	Bebe	Poly
Rank order determined with decided agonistic interactions	1	2	3
Rank order determined with grooming	1.5	1.5	3
Dominance index [Zumpe and Michael 1986]	72.10	49.05	39.50

Group r2	Diane	Sandy
Rank order determined with decided agonistic interactions	1	2
Rank order determined with grooming	1.5	1.5
Dominance index [Zumpe and Michael 1986]	76.25	23.75

Figure Legends

Fig. 1. Comparison of mean agonistic interaction/hour in the four *E. coronatus* groups during the non-breeding, breeding, gestation and birth season. Error bars ± 1 S.D.

Fig. 2. Comparison of mean agonistic interaction/hour in the two *E. rubriventer* groups during the non-breeding and the breeding season. Error bars ± 1 S.D.

Fig. 3. Distribution of agonistic interactions among the six study groups (*E. coronatus*, c1 to c4; *E. rubriventer*, r1 and r2) in the different behavioral contexts. The proportions of each type of agonistic interaction are indicated.

Fig. 1:

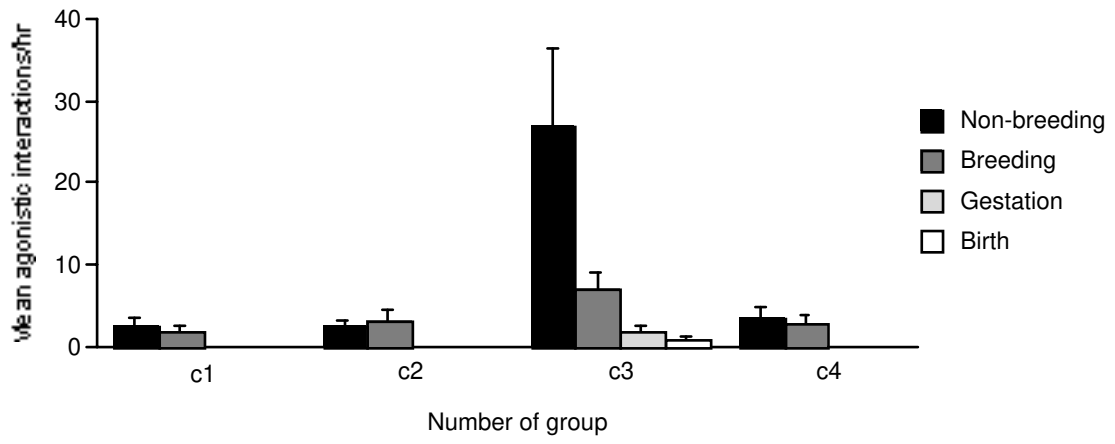


Fig. 2:

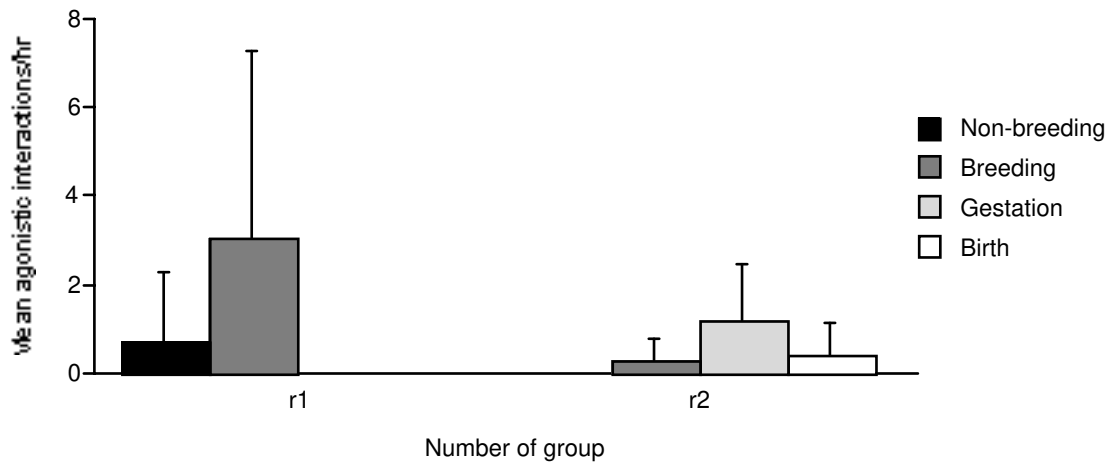


Fig. 3:

