

FEMALE DOMINANCE AND SOCIAL STRUCTURE IN ALAOTRAN GENTLE LEMURS

by

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(Acc. 29-VII-2003)

Summary

Lemur social systems have the striking social feature, that adult females consistently evoke submissive behaviour of adult males. In the Alaotran gentle lemur, *Hapalemur griseus alaotrensis*, however, female dominance has not been studied yet. Here we confirm female dominance over males on the basis of a 5-month field study of the social behaviour of four groups, in the Lake Alaotra marshland of eastern Madagascar. Further, we found that dominant individuals initiated aggressive interactions significantly more often than lower-ranking ones, they initiated group movements more often and higher-ranking individuals were groomed more often. The spatial configuration was remarkable, since individuals were closer in space to those more distant in rank.

1. Introduction

Female dominance is defined as the ability of all adult females to consistently evoke submissive behaviour from all adult males in dyadic agonistic inter-

⁴⁾ Field work by the first author was carried out through the Tripartite Commission under the Accord of the Jersey Wildlife Conservation Trust and the Government of Madagascar. Thanks are due to the governmental institutions of Madagascar for the permissions to conduct this study and to Dr T. Mutschler for helpful introduction into the field. Further, P.O. Waeber is grateful to Ramandraibè Marie Angèle of Andreba and to the field assistant Rajohonson Andrianirina Harry John Edmond. He was funded by G. & A. Claraz-Donation, A.H. Schultz-Foundation, Jutzler Jubiläums-Foundation and the Swiss Academy of Sciences. C.K. Hemelrijk is grateful to R. Pfeifer for continuous support and to the A.H. Schultz-Foundation for financial support. Both authors thank Dietmar Zinner and Bernard Thierry for comments on a former version of this paper.

actions (Pereira *et al.*, 1990). Female dominance over males is rare among mammals and primates in general, but common in many Malagasy lemurs (Lemuriformes, Primates) (Kappeler, 1993). Patterns of female dominance over males in higher primates have only been observed when females form coalitions to attack males (Smuts, 1987). Contrary to female feeding priority, female dominance is applicable to different behavioural contexts. It differs somewhat among different lemur species. For example, some species show clear female dominance such as ring-tailed lemurs (*Lemur catta*: Pereira *et al.*, 1990; Pereira & Kappeler, 1997), sifakas (*Propithecus* spp.: Kubzdela *et al.*, 1992; Wright, 1993), indris (*Indri indri*: Pollock, 1979), ruffed lemurs (*Varecia variegata*: Raps & White, 1995), blue-eyed black lemurs (*Eulemur macaco flavifrons*: Digby & Kahlenberg, 2002) and grey mouse lemurs (*Microcebus murinus*: Radespiel & Zimmermann, 2001) whereas others show weaker female dominance: conflicts are sometimes not decided and males show aggression against females also such as crowned lemurs (*Eulemur coronatus*: Pereira *et al.*, 1990) and aye-ayes (*Daubentonia madagascariensis*: Rendall, 1993). Some species have not been studied yet, such as the Aloatran gentle lemur *Hapalemur griseus alaotrensis*. We are the first to study its intersexual dominance relationships.

Further we examine the effect of dominance on the distribution of aggression, grooming, group-leading and spatial structure (*i.e.* the arrangement of individuals in space). A spatial structure according to dominance is of interest, because it may arise by self-organisation. This configuration may depend on the intensity of aggression (Hemelrijk, 1999) and it may differ depending on the 'decision rules' to attack others: if individuals attack others only when risks are low, they may end up with dominants in the centre and subordinates at the periphery and they are close to those of similar dominance rank; when individuals attack, however, to reduce the ambiguity of dominance relationships (Pagel & Dawkins, 1997) they will end up close to others of different rank (Hemelrijk, 1999, 2000). At a functional level, the spatial position may influence the degree of predation risk experienced (Hamilton, 1971) and the foraging possibilities of an individual (Rayor & Uetz, 1990).

Methods

Study area and animals

The study of *H. g. alaotrensis* was carried out in the wetlands of Lac Alaotra around Andreba, Madagascar (Mutschler & Feistner, 1995). The lake lies north of Ambatondrazaka. Its surface

TABLE 1. *Group composition*

Group	Sex	Body weight	Age class
1	m	1600 g	adult
	m	1125 g	adult
	m	1100 g	adult
	f	1000 g	adult
2	f	1400 g	adult
	m	1250 g	adult
	m	1075 g	adult
3	m	1475 g	adult
	f	1250 g	adult
	f	1150 g	adult
	f	600 g	juvenile
	m	600 g	juvenile
4	f	1500 g	adult
	m	1400 g	adult
	m	1225 g	adult
	f	1200 g	adult
	f	1100 g	adult
	m	925 g	subadult
	m	900 g	subadult
	f	850 g	subadult
	f	400 g	infant
	f	400 g	infant
	f	400 g	infant
	m	375 g	infant

Focal animals are indicated in bold.

area is 22,000 ha and the location of its centre point is 17°28'21''S and 48°31'40''E at an altitude of 750 m (Pidgeon, 1996). In January four groups of Gentle lemurs were captured by hand and weighed with a spring balance to an accuracy of ± 25 g (Table 1). Their sex was recorded and they were given neck collars to indicate individual identity and that of the group. Further, in order to trace the group a single adult was marked with a telemetry transmitter (Telonics).

Data collection

Data were collected from February to May 2001. All adult group members (7 males, 7 females of $>1,000$ g) served as focal animals. Every individual was selected randomly for a 60-min follow, and each one was observed for at least 10 hours. Observations were done in the early morning from 5.00-9.00 a.m. and in the late afternoon from 3.00-6.00 p.m.

All-occurrence sampling was used to record the following behaviour: agonistic interactions (see Table 2), the duration of a grooming bout (with its initiator and receiver), the order

TABLE 2. *Ethogram of Hapalemur griseus alaotrensis*

Behavioural class	Behavioural unit	Definition and description
Aggressive	open mouth display	Animal opens its mouth and displays its dentition for at least three seconds towards another group member.
	visual monitoring	Without moving its head for more than ten seconds an animal stares at another one of the same group.
	vocal threat	Animal gives a short and strong vocalisation towards a group member ('who-who').
	chase	Rapidly and closely following a conspecific, pursuing it some distance while it rapidly increases the distance.
	fight	Animal attacks a conspecific biting and grabbing with his arms at it, often together with a preceded vocal threat.
Submissive	avoid	Seemingly voluntary movements undertaken by some individuals when others either approached them or altered their position.
	whimper	Delicate whimper, in the context of foraging, i.e., one animal tries to take away from the others a piece of papyrus.
	'uiuiuiuiuiui'	Vocalisation during foraging; often together with a received preceded vocal threat.
	Vocal threat/rumble	Mixture between vocal threat and rumble; during foraging; often after receiving physical attack or an open mouth display.
Grooming	allogrooming	Animal uses the tooth comb and tongue to groom group members faces, necks, ears, and backs — those body parts, which cannot be self-groomed.
Vicinity	contact	Two or more animals are sitting in contact with each other (ignoring tail contact).

in which individuals crossed a water channel when at least 50% of the group was visible (but in a marshy area *ad libitum* sampling had to be used) and travel initiation. Travel initiation implied that in a stationary group an adult animal moved more than 1 m away from the group in a forward direction during at least one minute. If at least 50% of the group followed it, the initiation was declared successful.

Data analysis

To avoid bias in favour of certain conspicuous individuals, we used only focal animal data in our comparison of behavioural frequencies between the sexes.

Per group we determined a dominance hierarchy on the basis of a weighted dominance index (Hemelrijk & Gyax, unpubl. results) as follows: after generating a win/loss matrix, the Dominance Index DI, $DI = \#win/\#(win + lose)$, was calculated per cell. Per individual,

the average DI with all adult group members is computed. The higher the average Dominance Index of an individual, the higher its rank position in the group.

For correlations between matrices of social interactions we used the K_r -test (Hemelrijk, 1990). τ_{K_r} is a multivariate version of Kendall's τ ; it consists of within-row (individual) correlations that are summed over all rows, and thus takes individual variation (for example in grooming frequency) into account (Hemelrijk, 1990). τ_{K_r} has a value between -1 to $+1$. To calculate the probability of this statistic, we performed 500 permutations in case groups contained four adult individuals (in case of group three) and 1000 permutations for groups of five individuals (group 4). In tests for reciprocity/interchange, the right-sided 1-tailed probability-value is taken (Hemelrijk, 1990). We performed correlation tests only in groups with four or more individuals (in case of fewer individuals, tests cannot reach significance due to the small sample size). To combine the independent p -values of different groups we used the 'Fisher's Omnibus test' (Haccou & Meelis, 1992; Sokal & Rohlf, 1981, p. 623).

We tested whether individuals directed more behavioural acts to, or received them from partners, the higher the dominance rank of the partner. For this we correlated a matrix of behavioural acts with a matrix of the dominance of the partner and a matrix of the rank-distance of the pair (Hemelrijk, 1990).

Results

There were 260 inter sexual conflicts. All but one had a clear winner. Most of these (93.4%) concerned food. Females won more fights than males did (Mann-Whitney U : $N_m = 7$, $N_f = 7$, $U = 0.0$, $p = 0.0017$; 2-tailed, Fig. 1). Also the dominance interactions without display of aggression were won by females more often than by males (Mann-Whitney U : $N_m = 7$, $N_f = 7$, $U = 0.0$, $p = 0.0017$; 2-tailed, Fig. 1). Further, females displayed submission less often than males, namely in only 25 of 173 inter sexual interactions with submission (Mann-Whitney U : $N_m = 7$, $N_f = 7$, $U = 0.0$, $p = 0.0017$;

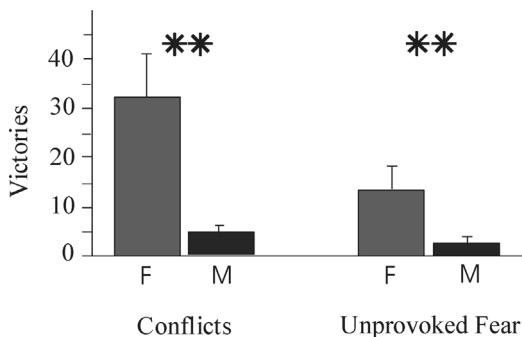


Fig. 1. Inter sexual interactions: conflicts and unprovoked fear where only submission was displayed (mean and SE). F: Females; M: Males. ***: $p < 0.01$.

TABLE 3. *Kendall rank correlation between agonistic behaviour, grooming and group leading*

	Group-identity	N	Kendall τ	p	Fisher Combination test, χ^2
Association between losing and grooming					
	3	4	0.833	0.1045	10.8573*
	4	5	0.8	0.042	
Association between losing and being groomed					
	3	4	-0.833	0.1045	9.5811*
	4	5	-0.7	0.0795	
Association between dominance and aggression initiated					
	3	4	0.333	0.375	11.6183*
	4	5	1	0.008	
Association between dominance and acting aggressive					
	3	4	0.333	0.375	11.6183*
	4	5	1	0.008	
Association between dominance and being groomed					
	3	4	0.833	0.1045	9.5811*
	4	5	0.7	0.0795	
Association between dominance and leading in a marshy area					
	3	4	1	0.042	9.1778
	4	5	0.4	0.242	
Association between dominance and success-rate of initiation					
	3	4	0.667	0.167	7.8707
	4	5	0.6	0.117	
Association between win and acting aggressively					
	3	4	0.947	0.0339	17.3653*
	4	5	0.898	0.005	
Association between win and aggression initiated					
	3	4	0.947	0.0319	17.9332*
	4	5	0.898	0.004	
Association between losing and received aggression					
	3	4	0.71	0.0719	13.8348*
	4	5	0.621	0.016	
Association between grooming and received aggression					
	3	4	1	0.4311	4.6590
	4	5	0.816	0.2258	
Association between acting aggressive and aggression initiated					
	3	4	1	0.042	15.9968*
	4	5	1	0.242	

*: $p < 0.05$.

2-tailed). Similarly when looking at the complete group without distinguishing between the sexes, higher-ranking individuals displayed aggression more frequently and initiated agonistic interactions more often (Table 3).

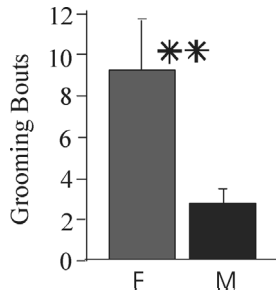


Fig. 2. Being groomed by the opposite sex (mean and SE of number of bouts). F: Females; M: Males. **: $p < 0.01$.

TABLE 4. Results of matrix τ_{Kr} test

Association between	Group identity	N	τ_{Kr}	p	Fisher Combination test, χ^2
Partner rank and grooming	3	4	0.633	0.1737	9.5327*
	4	5	0.747	0.049	
Grooming and acting aggressively	3	4	-0.816	0.0579	10.4941*
	4	5	-0.617	0.0909	
Rank distance and being groomed	3	4	0	0.5429	6.2286
	4	5	0.641	0.0399	
Rank distance and being in contact	3	4	-0.918	0.0499	9.6382*
	4	5	-0.303	0.1618	

*: $p < 0.05$.

As regards grooming, it appeared that females were groomed more often by males than *vice versa* (Mann-Whitney U : $N_m = 7$, $N_f = 7$, $U = 49$, $p = 0.0017$; 2-tailed, Fig. 2) and related to this, that higher ranking individuals were groomed more often (Table 3). Correspondingly, individuals spent more time grooming other group members, if they lost fights more often and they themselves were groomed less often (Table 3). Further, individuals groomed partners more often the higher the rank of the partner (Table 4) and related to this, they were less often aggressive to those partners which they groomed more often (Table 4).

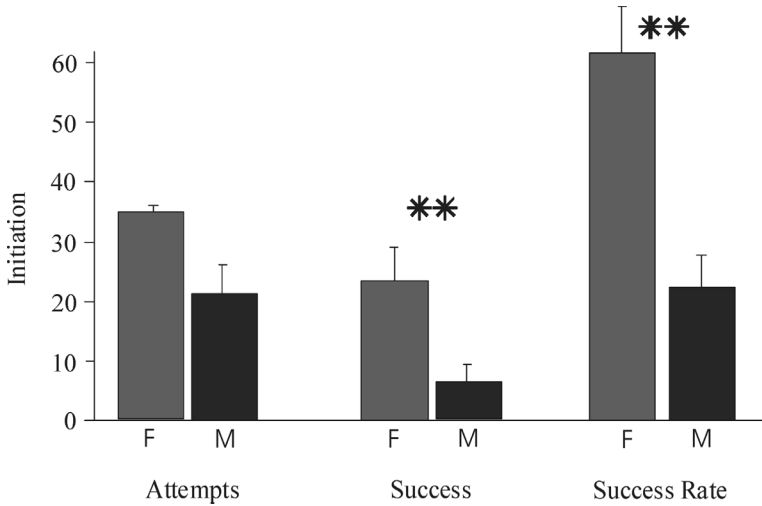


Fig. 3. Travel initiation of group movement: total attempts, successful initiations and success rate of initiation (mean and SE). F: Females; M: Males. **: $p < 0.01$.

In contrast to our expectations regarding spatial structure, those individuals were closer together in space, the larger (instead of smaller) the rank distance between them (Table 4).

As regards group leading, higher-ranking individuals led the group more frequently (Table 3), and although both sexes attempted to initiate movements equally often (Mann-Whitney U : $N_m = 7$, $N_f = 7$, $U = 14$, $p = 0.1797$; 2-tailed, Fig. 3), females were more successful than males (Mann-Whitney U : $N_m = 7$, $N_f = 7$, $U = 4.0$, $p = 0.0088$; 2-tailed, Fig. 3). Thus, the percentage of successful initiations of all attempts were higher for females (Mann-Whitney U : $N_m = 7$, $N_f = 7$, $U = 4.0$, $p = 0.0088$; 2-tailed, Fig. 3). Group leading depended, however, on the terrain: whereas in a marshy area, females led the group significantly more often than males (Mann-Whitney U : $N_m = 7$, $N_f = 7$, $U = 8.5$, $p = 0.0409$; 2-tailed, Fig. 4), over water-channels both sexes led the group equally often (Mann-Whitney U : $N_1 = 7$, $N_2 = 7$, $U = 11.0$, $p = 0.0845$; two-tailed, Fig. 4).

Discussion

Like in ringtailed lemurs (Pereira *et al.*, 1990), in groups of *Hapalemur griseus alaotrensis* inter sexual agonistic encounters always had a clear win-

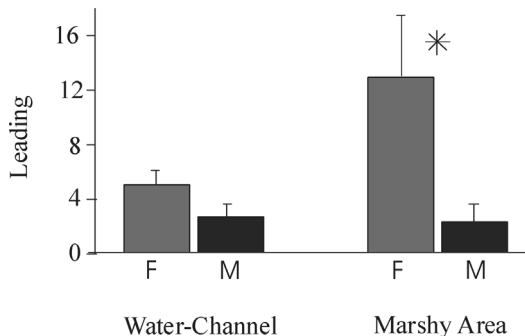


Fig. 4. Frequency of group leading over a water-channel and in a marshy area (mean and SE). F: Females; M: Males. **: $p < 0.05$.

ner. Our data show that in each of the four study groups, females are clearly dominant over males. Aggressive behaviour occurred in more than 23% of all inter sexual interactions. In inter sexual interactions without aggression females were able to elicit a submissive signal from adult males in 83 percent of the cases. Thus, in most interactions females do not even need to display aggression to evoke submission in males.

Long-term field studies on other lemur species have revealed that major social changes in dominance occur prior to and during the mating season, because food availability changes (Jolly, 1966; Martin, 1973; Richard, 1974). Because we collected data only in the period from February to May (and not in the mating season), it is unclear whether females dominate males year round. However, food supply is stable during the year (Mutschler, 1999) and therefore, female dominance probably does not change much.

As most aggression occurred in the context of feeding, our findings may only reflect female priority to food, but no female dominance in general. Nevertheless, the grooming and leading pattern gives further support for female dominance over males.

Females initiated and continued to lead the group movement more often than males. The leading position remained fixed during travelling. What remains unclear is whether the initiator and the leader were always the same individual. For instance, in ring-tailed lemurs leadership could change between initiation and travel continuation (Jolly, 1966). Leadership depended, however, on the terrain. Whereas over marshy areas, females led the group most often, over water-channels groups were led by both sexes equally often. This is probably due to a dislike of contact with water.

We did not find a spatial arrangement with dominants in the centre as found in an individual-based model, called DomWorld, in case individuals attack others mainly when risks are low (Hemelrijk, 2000). In contrast, Gentle lemurs appeared to be closer to those partners the larger the difference in rank to them. This corresponds to the spatial structure found in the model in case agents attack others to 'reduce the ambiguity' of their relationships to them and they stop attacking once relationships are clear (Pagel & Dawkins, 1997). In the groups studied here this spatial configuration cannot be attributed entirely to sex differences or kin relationships, because apart from low-ranking males being close to high-ranking females, also rank-distant females are sometimes close together. These females are unlikely to be kin, because maturing females usually leave the group before reaching adulthood (Mutschler, 1999).

Remarkably, this spatial structure is not reflected in the distribution of grooming behaviour. Instead grooming appears to be directed towards higher-ranking individuals. This corresponds with findings of baboons (Seyfarth, 1976) and chimpanzees (Hemelrijk & Ek, 1991). Grooming higher-ranking individuals may function to protect the groomers from potential aggression by these high-ranking partners (Silk, 1982), because grooming reduces tension (Terry, 1970).

Clearly, compared to the social structure of Anthropoid Primates that of Aloatran gentle lemurs is reversed: Apart from being dominant over males, females are more aggressive, they are groomed more often and they lead the group more often than males. In order to better understand the association between dominance and these acts, it would be of great interest to obtain information whether these associations hold universally. In other words, are females of other species with female dominance also more often aggressive, do they lead the group more often and are they groomed more often than males are?

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