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DOMINANCE RELATIONSHIPS IN A *LEMUR FULVUS* GROUP

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Female dominance is considered to be a characteristic of social organization in many prosimian species (Richard, 1987). Explanatory models proposed for female dominance are based mainly on energetic costs of breeding during a short annual season (see Richard & Nicoll, 1987).

In the Lemuridae, a family of gregarious malagasy prosimians, female dominance was first described by Jolly (1966) in ringtailed lemurs, *Lemur catta*. *L. catta* females were reported to win most agonistic encounters with males, and to have priority of access to feeding and drinking sites. However, conventional criteria based on the direction of asymmetric dyadic agonistic interactions (Bernstein, 1981) proved to be difficult to use for other *Lemur* species, such as the more common *L. fulvus*, due to the low frequency and intensity of spontaneous aggression (Harrington, 1975 ; Sussman, 1975 ; Tattersall, 1977). Consequently, dominance in these species has remained little documented in field studies.

More recent data from semi free-ranging groups (Pereira *et al.*, 1990) indicate considerable interspecific variability in dominance relationships within the Lemuridae. Compared to unambiguous « female-dominant » species like *L. catta*, other species such as *L. coronatus* and *L. fulvus* appear to show different patterns of dominance, without any systematic effect of gender.

Here, social dominance was studied in *L. fulvus mayottensis* by examining factors related to aggression and to priority of access to food in two competitive contexts. Like most other Lemuridae, *L. fulvus mayottensis* lives in multimale groups, but is characterized by a greater lability of social units (Tattersall, 1983). The aims of the study were to test the hypothesis of female dominance, using experimental situations designed to increase interindividual competition and aggression. These situations were adapted from those traditionally used to measure dominance in other primates (e.g. macaques, Belzung & Anderson, 1986 ; Boelkins, 1967).

MATERIAL

The study was conducted on a group of *L. fulvus mayottensis*, at the Centre de Primatologie de l'Université Louis Pasteur de Strasbourg, in a spacious

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indoor-outdoor cage. The group contained two adult males (B, M), one subadult male (f), two adult females (H, V), and the subadult daughter (h) of one of the adult females. This group has evolved from an original group formed three years before from presumably unrelated wild or captive group-reared adults. The animals received commercial primate pellets and water *ad libitum*.

METHODS

The group was studied in two experimental situations involving limited access to 1) a box containing banana slices, and 2) a bottle of orange juice. Both apparatus were attached to the wire-mesh of the cage. In order to reach the banana slices, the animals had to extend an arm through the wire-mesh. Drinking from the bottle was via a metal spout.

For each situation, a series of 10 experimental sessions was conducted, during the non-breeding season. Each session within a series was separated by 12 to 48 hours. The following behavioural data were collected during each session, using checksheets marked off into 30 sec-intervals :

- the identity of the animals present at the food-box or at the bottle, that is, subjects standing within one meter from the apparatus and attempting to gain access to the resource (« one-zero sampling », Altmann, 1974),
- the acquisition of banana slices or of orange juice,
- all occurrences of aggressive interactions in the immediate vicinity of the resource (noting initiator, receiver, and outcome of aggression : fleeing, counter-aggression, or no response).

Data collection lasted until all banana slices had been eaten or until all individuals had drank for at least ten 30 sec intervals, which usually took about thirty minutes.

Aggressive interactions were also recorded using the same observation procedure for 10 hours during non-experimental sessions.

RESULTS

No clear dominance of one individual over all the others appeared in terms of access to banana slices or orange juice.

During feeding tests, four individuals showed similar degrees of access to the bananas, whereas two others, namely the two males M and f, virtually never obtained any (Fig. 1). The male M was prevented from approaching by frequent aggression from B, whereas f was frequently present at the food-box but was rarely successful at grasping fruit, despite frequent attempts.

During drinking tests all individuals, excepted the male M, had access to the bottle for several periods throughout each session (Fig. 2). On some occasions several subjects were present simultaneously at the bottle and drank together or in alternation. Such mutual tolerance was especially characteristic of the females. However, all individuals showed one main period of drinking sooner or later during the test. The females h and V had priority of access at the start of each test. The male B and the male f drank next, while the male M was always last to drink, once all others were satiated. Rank order based on either total drinking duration

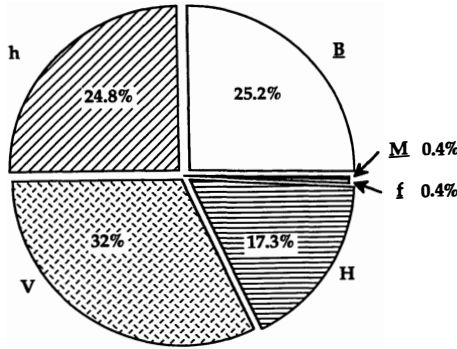


Figure 1. — Distribution of banana slices among individuals in the group. Males are underlined.

or drinking duration during the first five minutes of the test was not significantly correlated with the feeding rank order (Spearman rank-correlation test, $N = 6$, $r_s = 0.01 / r_s = 0.52$, n.s.).

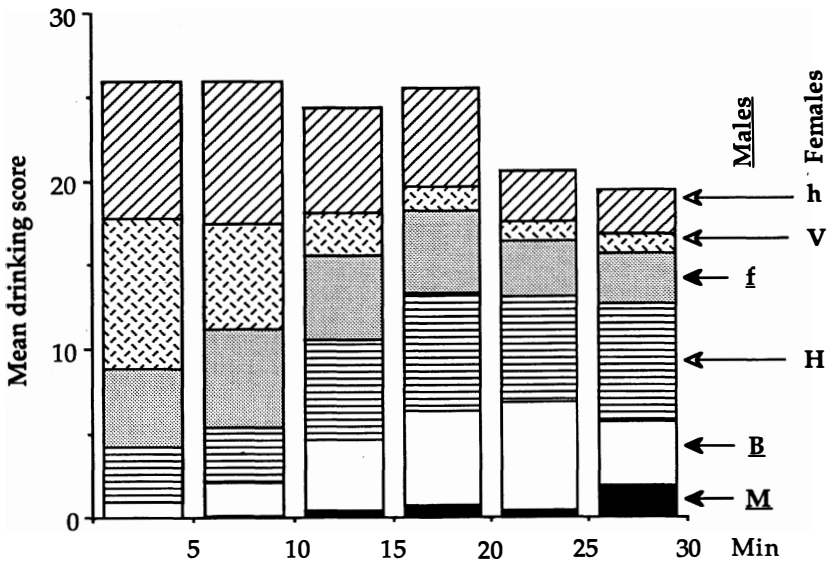


Figure 2. — Mean individual drinking scores during the 10 experimental sessions (number of 30-sec intervals). Males are underlined.

Eighty percent of all aggressive interactions occurring at the drinking or feeding site were unidirectional, with no marked behavioural reaction by the receiver. Submissive behaviours were never observed, and displacement of one individual by another was very rarely observed, and only in males. Aggressive acts

were most frequently initiated by the male B and were directed towards the male M, resulting in M fleeing without counter-aggression (Table I). The male M virtually never showed aggression against females, whereas the majority of this type of aggression was initiated by B. Although only a low proportion of aggressive episodes between B and a female resulted in a withdrawal, the « winner » was more frequently the male. The subadult male f received aggression from females as often as he threatened them, with the exception of H. Intrafemale aggression was more limited both in frequency and intensity, consisting usually of vocal threats or mild cuffs. Thus, in the absence of decisive aggression, no dominance hierarchy could be inferred from the analysis of intrafemale aggressive interactions. In order to correlate the feeding and drinking rank orders with a rank order based on aggression, we used Zumpe and Michael's dominance index (1986). This index, based on the proportions of aggressive and submissive behaviors (fleeing in the present study) between all possible pairs of animals was found to be concordant with other dominance measures, and it is suitable for situations where aggression is infrequent. No significant correlations emerged from this analysis, although all were positive (Spearman, $N = 6$, feeding test : $r_s = 0.58$, drinking test $r_s = 0.71$ for total drinking duration and $r_s = 0.31$ for drinking during the first five minutes).

During non-testing periods, aggression was even more infrequent, and the only dominance relation that appeared clearly was between the two males B and M, again showing that B was dominant.

DISCUSSION

In the group of *L. fulvus mayottensis* studied here, we found no agonistic dominance or feeding priority of one sex relative to the other. Priority of access to an incentive in a restricted-access situation appeared in some *L. fulvus* individuals, but the feeding rank order varied between situations and was not significantly correlated with rank order based on aggressive interactions.

The most striking result was the marked dominance relationship observed between the two adult males, which was evident from the asymmetry of aggression and displacement as well as in priority of access to a limited food resource. In the context of another food acquisition task — opening a baited food-box — a similar dominance-subordination relationship occurred between adult male *L. fulvus mayottensis*, whereas female dominance emerged in *L. macaco* and *L. catta* (Fornasieri *et al.*, 1990). Moreover, increased evidence of intermale dominance appeared from long-term observations of *L. fulvus* social behaviour, with escalating aggression occurring during the breeding season (Colquhoun, 1987 ; Fornasieri, 1991).

Apart from adult males, social conflict in the group was characterized by infrequent decisive interactions. However, when considering only interactions intense enough to result in withdrawal, these were performed most frequently by a male, in agreement with the results of Pereira *et al.* (1990) in *L. fulvus rufus*. In *L. fulvus* females, social relationships seem to be especially influenced by preferential associations with individual males (see Fornasieri, 1991) and by occasional episodes of social rejection. The phenomenon of « targeting aggression » (Vick & Pereira, 1989), initiated by most group-members against one individual and

TABLE I

Aggression in limited-access situation to a feeding resource (pooled data for feeding and drinking tests).

Top line : number of aggressive acts initiated/received ; bottom line : percentage of decisive aggressions initiated/received (aggression resulting in withdrawal). Males are underlined.

	<u>M</u>	<u>f</u>	H	V	h
<u>B</u>	134 / 1	27 / 0	54 / 0	128 / 9	25 / 6
	63 0	7 -	20 0	7 44	8 17
<u>M</u>		9 / 6 0 50	2 / 0 0 -	0 / 0 - -	0 / 0 - -
		<u>f</u>	54 / 7 20 0	55 / 41 4 0	53 / 52 2 2
			H	3 / 4 0 0	0 / 0 - -
				V	2 / 16 0 0

resulting in the latter's exclusion from the group, has been described in all captive rearing conditions and in the field, and appears to be an important social regulatory mechanism in Lemuridae.

In conclusion, the absence of any significant correlation between the measures used to evaluate dominance in the two situations studied here raises the problem of the nature of social dominance in the Lemuridae, in which the forms of aggression limit the applicability of traditional methods of deciding of dominance used in other primates. Compared to most other primates which respond to restricted food-access situations by increased competition, *L. fulvus*

mayottensis appear to show only mild aggression and greater tolerance in similar contexts. In contrast to *L. catta*, which exhibit a clear dominance of females over males, as well as a marked dominance hierarchy among females and to a lesser extent in males (Kappeler, 1990), in *L. fulvus mayottensis*, only males could be ranked reliably in terms of dominance status. Other dominance relationships varied greatly as a function of the criteria used and the situation, suggesting low interindividual rank order differences in terms of agonistic or feeding precedence in this species.

RÉSUMÉ

Une étude des relations de dominance a été réalisée dans un groupe de *Lemur fulvus mayottensis* élevé au Centre de Primatologie de Strasbourg. L'analyse a porté sur différents critères relatifs à l'agression, ainsi qu'à la présence alimentaire lors de l'accès à une source de nourriture ou de boisson. Les résultats révèlent essentiellement une relation de dominance marquée entre les deux mâles adultes du groupe, ainsi qu'une absence de dominance des femelles sur les mâles contrairement au schéma classiquement décrit chez les Lémuridés ; ils sont discutés dans le cadre de données récentes concernant l'organisation sociale de ces espèces.

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