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Does Agonistic Dominance Imply Feeding Priority in Lemurs? A Study in *Eulemur fulvus mayottensis*

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We studied agonistic dominance and priority of access to a limited drinking resource in two captive groups of Eulemur fulvus mayottensis. *Gender is not systematically related to agonistic dominance or to drinking priority. The dominance hierarchy obtained in the drinking competition test is correlated with the baseline hierarchy in the absence of induced competition, but not with drinking priority. We analyze results within the framework of recent dicussions on female dominance in Malagasy prosimians.*

KEY WORDS: *Eulemur fulvus*; social dominance; drinking priority; scent marking.

INTRODUCTION

Female dominance was long thought to be a constant in Malagasy prosimian social organization, based on studies of a few species: *Indri indri* (Pollock, 1979), *Phaner furcifer* (Charles-Dominique and Petter, 1980), *Microcebus murinus* (Perret, 1982), *Lemur catta* (Jolly, 1984), *Propithecus verreauxi* (Richard and Nicoll, 1987), and *Varecia variegata* (Kaufman, 1991). In the group-living species of *Eulemur* and *Varecia*, the referent for female dominance is *Lemur catta*, first described by Jolly (1966) and confirmed by subsequent studies of free- or semifree-ranging groups (Budnitz and Dainis, 1975; Kappeler, 1990a; Kaufman, 1991; Sussman, 1991; Taylor and Suss-

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man, 1985; Sauther, 1993). Further studies document agonistic female dominance in some lemur species [*L. catta* (Kappeler, 1990b; Pereira *et al.*, 1990); *E. macaco* (Fornasieri *et al.*, 1993)] but not others, notably in the different subspecies of *Eulemur fulvus*, due mainly to the scarcity of aggressive episodes (Sussman, 1977; Tattersall, 1982, 1983; Pereira *et al.*, 1990). In fact, almost no aggressive competition has been observed in natural groups of *E. fulvus*, even for access to food. On the basis of recent studies on semicaptive groups of different lemur species, it is now generally accepted that female dominance is not systematic in the Lemuridae and that patterns of social relationships are probably more various and complex than previously thought (Kappeler, 1990b; Pereira *et al.*, 1990).

True female dominance is characterized by consistent directionality of agonism in both feeding and nonfeeding contexts: sleeping, grooming, and spatial distribution. Such dominance is generally associated with female feeding priority (Jolly, 1984). However, to our knowledge, feeding priority has not been quantified; studies showing feeding priority take into account agonistic acts but not the actual access to food resources (Fornasieri *et al.*, 1993). In fact, the nature and function of female dominance among lemur species remain uncertain (Sauther, 1993), as does the relation between this dominance type and feeding priority. Therefore, we analyzed agonistic dominance and priority of access to a limited drinking resource in a lemur species among which female dominance had not been observed: the brown lemur, *E. fulvus mayottensis*. We compared the dominance hierarchy obtained in a competitive drinking situation with the baseline hierarchy in the absence of induced competition. We analyzed the correlation between agonistic dominance established under standard conditions and competition for access to a drinking resource and drinking priority in different groups.

METHODS

Subjects

We studied two groups of *E. fulvus mayottensis* in indoor (6.00 × 2.10 × 2.60-m)–outdoor (8.00 × 2.90 × 2.60-m) enclosures at the Centre de Primatologie de l'Université de Strasbourg (CPUS). The groups were formed from wild-born (wb) or captive group-reared adults. Group 1 was the original group. At the start of the study, it contained five adults: two males, M1 (wb) and his son M2 (3 years old): and three females, F1 (wb), F2 (wb), and F3, the daughter of F2 (3 years old). The group had been established for several years. Group 2 was formed from four wild-born adult females (F4, F5, F6, F7) removed from the original group because of injuries received during targeting aggression (Vick and Pereira, 1989) and a new adult male (M3, 7 years old). At the beginning of the study, the group had been together for 1 year. The composition of Group 2 varied during the study: F6 died after the first series of tests, and F7 was ostracized during series 1 and 2.

Food (commercial primate pellets) was available *ad libitum*, and keepers provided fresh fruit and vegetables twice weekly outside the observation periods. We identified individuals by differences in coat color and condition, tail shape, and facial scars.

Procedure

The study consisted of 10-session series of baseline and experimental observations, conducted every 2 months. We conducted five series on Group 1 (from November to July) and three on Group 2 (December to April). Each session consisted of a 1-hr baseline observation, followed by a 1-hr drinking test. Two sessions within a series were separated by 24 to 48 hr.

Baseline Observations

During baseline observations, we recorded agonistic encounters via the "all occurrences" and "behavior-dependent sampling" methods (Altmann, 1974). For each interaction, we recorded the form of the aggression—threat, cuff, bite, approach/flee, chase; its outcome—counteraggression, jumping or running away, simply looking away, no behavioral response; and the identity of the opponents. From these data, we calculated a dominance index (Zumpe and Michael, 1986) for each individual and each control series. This index, expressed as a percentage, is based on the number and the direction of aggressive and submissive behaviors exchanged by each individual with all other group members and is especially well suited to small groups showing infrequent aggression. We used approach-avoidance interactions to characterize submissive behaviors because no submissive facial expressions or specific vocalizations are observed in *E. fulvus*. (Fornasieri, 1991). We recorded all occurrences of scent marking (anogenital rubbing) during the sessions.

Drinking Tests

We presented each group with a bottle of orange juice equipped with a metal spout and attached to the wire mesh of the cage, so that one individual at a time could cling to the wire mesh and drink from the bottle. During each experimental session, we used one-zero sampling (Altmann, 1974) at 15-sec intervals to identify subjects engaged in drinking or standing within ≤1 m of the apparatus and trying to gain access to the bottle. When two animals drank simultaneously, each was scored separately. For each subject and for each series, we calculated two kinds of drinking scores across the 10 sessions in order to evaluate drinking priority: mean total number of drinking intervals and mean number of drinking intervals during the first 5 min of the test. We also recorded agonistic interactions during the drinking tests via the procedure described above in order to calculate individual experimental dominance indices. We recorded all occurrences of scent marking.

We conducted a series of test and control observations 1 year later on Group 1 when female F1 was removed from the group while female F2 was lactating.

RESULTS

Group 1

Agonistic Dominance Under Baseline and Experimental Conditions

No agonistic dominance of females over males appeared in Group 1, under either baseline or experimental conditions (Fig. 1). Individual dominance indices showed more variability during the baseline condition than during the drinking tests, and rank order differences were also greater during baseline periods. Generally, the competitive drinking situation resulted in a significant increase in aggression (mean frequency during/outside tests: M1, 69.5/17.2; M2, 61.2/4.7; F1, 11.5/1.5; F2, 86/3.2; F3, 135.5/4.2). Under both conditions, a male (M1) obtained the highest dominance indices, whereas a female (F2) obtained the lowest. An important difference in dominance indices appeared between the two males, with a high rank for the oldest, M1, and a low one for M2. During the first session, which coincided with the mating season, M2 increased his dominance index over M1 and all other group members and scored highest in the baseline dominance hierarchy. This temporary agonistic dominance was accompanied by an increased aggression rate, mostly toward females and during sexual approaches. Females were distributed across the middle ranks, with a consistent hierarchy during drinking tests (in decreasing order: F3, F1, F2), with some reversals in the first and last baseline series.

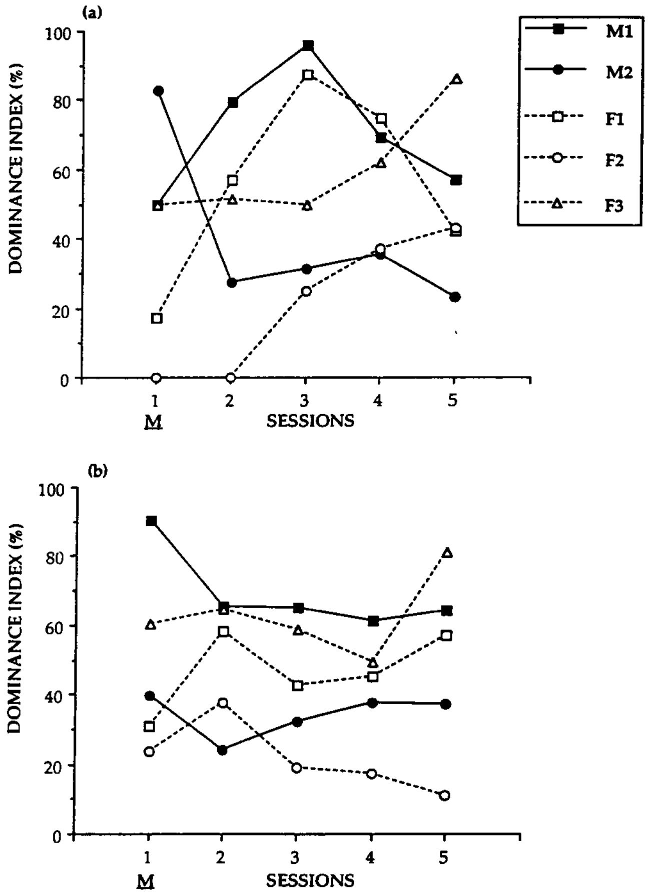

Fig. 1. Pattern of dominance indices (a) under baseline conditions and (b) during drinking tests. M: mating period.

Mean dominance indices (calculated over the five sessions) during baseline observations are positively correlated with those obtained during drinking tests (Table I). The mean baseline dominance indices are correlated with the mean baseline marking frequencies, though the same correlation did not appear under experimental condition. The test situation induced a striking increase in marking rates in males but not in females (Table I). During the first session, we recorded a reversal in dominance indices in males under baseline conditions. This reversal was not observed

Table I. Mean Drinking Scores, Dominance Indices, and Scent-Marking Frequencies (SD) in Group 1

	Drinking score		Dominance index		Marking frequency	
Subject	First 5 min	Total	Experimental	Baseline	Baseline	Experimental
M1	0.4 (3.5)	9.6 (3.5)	69.2 (12)	70.3 (18.2)	39.2 (17.7)	148.6 (82)
M2	0.9 (0.8)	7.1 (2.7)	34 (6.2)	39.9 (24.4)	10.6 (7.8)	34.2 (24.4)
F1	10.9 (6.4)	13.9 (1.8)	46.7 (11.3)	55.7 (27.5)	20.4 (28.7)	8.8 (17.4)
F2	6.8 (5.4)	13 (4.5)	21.6 (9.9)	21 (20)	3.2 (2.1)	1.6 (2.5)
F3	31 (4.8)	18 (2.4)	65.3 (9)	59.9 (15.4)	20 (13.1)	19.6 (11.3)
Spearman rho	0.9 (P = 0.03)		0.2 (ns)	1	0.9 (P = 0.03)	
		-0.1 (ns)			0.7 (ns)	

for marking activity, M1 maintained a highest marking frequency compared to M2.

Drinking Priority

Over the five sessions, the females showed a general priority of access to the orange juice. F3 consistently obtained the highest drinking score during the first 5 min (Fig. 2a) and almost always the highest total drinking score (Fig. 2b). Differences among the females in the amount of time in possession of the resource were low over the whole test, but F3 had priority at the start of the sessions, drinking twice as much as F1 and F2.

The males showed similar drinking scores, but they came last, behind the females on both measures that are significantly correlated for the whole group ($r_s = 0.9$, $P = 0.03$) (Table I). The males could not maintain access to the bottle for very long during the first part of the sessions, despite their attempts to prevent the females from drinking. The males spent more time drinking when the females were satiated and had abandoned the bottle. The older male then constantly tried to keep the other away. In general, whenever M1 drank, he tried to monopolize the bottle by pushing the others' muzzles away from the spout, which sometimes resulted in aggression. The mating period does not appear to influence drinking priority.

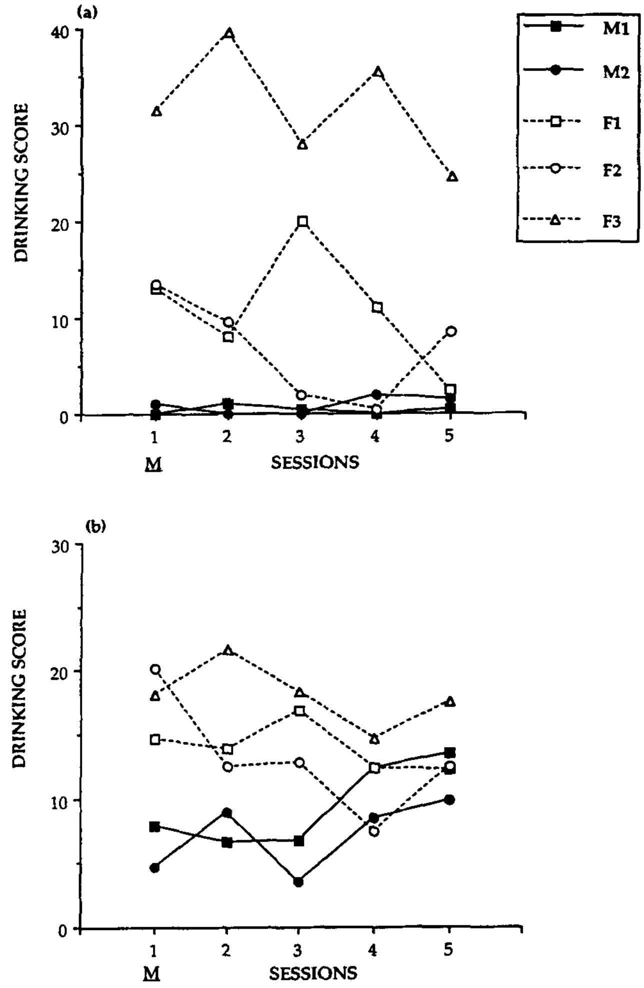

Fig. 2. Pattern of (a) drinking scores during the first 5 min of the test and (b) total drinking scores. M: mating period.

Aggression in relation to competition for the resource was not solely intrasexual, (Table II). Agonistic interactions occurred between the males (M1 toward M2), between females (mainly F3 toward F1), and between males and females (M2 and F1).

Neither drinking scores at the start of the test, when motivation for drinking and competition were assumed to be highest, nor total drinking

Table II. Total Number and Percentage of Aggressive Acts Under Drinking Conditions

	Aggressee					
Aggressor	M1	M2	F1	F2	F3	Total
M1		229 (10.8%)	107 (5%)	114 (5.2%)	71 (3.2%)	521 (24.2%)
M2	22 (1%)		233 (10.8%)	117 (5.4%)	58 (2.8%)	430 (20%)
F1	36 (1.7%)	247 (11.5%)		116 (5.5%)	63 (2.9%)	462 (21.6%)
F2	5 (0.2%)	20 (0.9%)	11 (0.5%)		14 (0.7%)	50 (2.3%)
F3	20 (0.9%)	175 (8.1%)	449 (20.9%)	42 (2%)		686 (31.9%)
Total	83 (3.8%)	671 (31.3%)	800 (37.2%)	389 (18.1%)	206 (9.6%)	2149 (100%)

scores are correlated with agonistic dominance in the same situation (respectively, $r_s = -0.1$, $r_s = 0.2$, n.s.).

During the second test period, when female F2 was lactating, we obtained similar results regarding dominance indices in the two situations and regarding drinking priority.

Group 2

Agonistic Dominance in Baseline and Experimental Conditions

The male showed the highest dominance index in all of the experimental series and all except one baseline series (Table III). F4 consistently outranked the other females in both conditions when three females were present, in particular F5, which was always present in the group during the study. When the group contained only F4 and F5, the rank difference between them was reduced and reversed during drinking. The two other females, F6 (series 1) and F7 (series 3), held intermediate dominance ranks, close to F4.

Table III. Drinking Scores, Dominance Indices, and Scent-Marking Frequencies in Group 2

		Drinking score		Dominance index		Marking frequency	
Series	Subject	First 5 min	Total	Experimental	Baseline	Experimental	Baseline
1	M3	66	15.9	59.6	60.9	38	5
	F4	21	12.6	44.9	57.0	0	8
	F5	4	11.2	21.7	6.2	0	0
	F6	15	10.7	27.0	0	0	2
2	M3	60	20.4	75.5	42.8	30	0
	F4	30	14.8	43.5	65.4	1	3
	F5	4	13.7	49.6	37.5	1	1
3	M3	77	17.5	71.5	72.1	86	51
	F4	12	19.6	49.4	48.2	4	0
	F5	1	8.5	16.1	27.6	21	1
	F7	10	14.1	18.3	20.8	7	8

Drinking Priority

Considering the two drinking scores, a marked priority of access to the bottle emerged for the male and, to a lesser extent, for F4, regardless of group composition (Table III). Other females had to wait until the latter showed diminished interest in the bottle before they could gain access to it. Attempts by F4 to displace the male during the first few minutes of the tests resulted in dissuasive counteraggression.

Aggression was more frequent in Group 2 than in Group 1, due mostly to the male. The highest-ranking female, F4, was the most frequent recipient of the male's aggression, while F5's presence was tolerated by the male when he was drinking. Generally, M3 had a higher marking rate under experimental conditions, which induced a striking increase in marking activity.

DISCUSSION

Our study was carried out on small captive groups of partially unrelated, lemeurs whose ages are unknown. Further, the number of males differed between the two groups, and the composition of Group 2 varied over time. Accordingly, the study should be considered as a preliminary investigation of brown lemur social dynamics. It may be noted, however, that a recent study on *E. fulvus rufus* showed that, contrary to other lemur species, sex and kinship have no significant effect on the distribution of agonistic interactions (Kappeler, 1993).

Our findings supplement previous studies (Pereira *et al.*, 1990) which showed that the social organization of the brown lemur is not based on female dominance. In the CPUS groups of *E. fulvus mayottensis*, intersexual agonistic dominance varied with group composition. In the two-male group, no clear pattern of sexual dominance appeared: both males and females obtained low and high dominance indices. However, the highest-ranking animal was a male. The most striking result in this group is a marked dominance relationship between the two males. In the one-male group, the male was consistently dominant over females. In both groups, clear differences in social status appeared between some females. Aggression rates were substantially increased by the introduction of the limited drinking resource, with subsequently greater differences in individual dominance indices. However, the baseline dominance hierarchy appeared to be maintained during drinking tests, as indicated by the significant correlation between the two measures. The dominance hierarchy appears to be stable over time in the experimental situation but more variable under neutral condition. In the latter case, we observed a dominance reversal between males in the two-male group during the mating season.

Scent marking rates are generally correlated with dominance status under baseline conditions, which data agree with those from previous studies on *E. fulvus* (Fornasieri and Roeder, 1992). However, the test situation generally led to an increase in marking rates in males and a decrease in females, implying different use of scent marking between sexes. Among *Lemur catta*, Kappeler (1990a) found a clear positive correlation between rank and the frequency of scent marking in males but not in females. Our study implies that male scent marks may serve in indirect intrasexual competition by reducing sexual activity. In Group 1, we noted a reversal in the dominance hierarchy between the two males under baseline condition in series 1, but no modification in their marking rates: M1 maintained the highest marking frequency. Both males mated. These observations do not support the hypothesis of intrasexual competition. The fact that males always increase their marking activity during the test condition irrespective of their social statuses indicates that marking activity appears to be a correlate of general increase in arousal.

The second point to emerge from our study that agonistic dominance is not always correlated with drinking priority. In unambiguously female-dominant prosimian species—*Lemur catta*, *Eulemur macaco*, and *Indri indri*—females consistently supplant males at feeding sites (Jolly, 1984; Pollock, 1979; Fornasieri *et al.*, 1993): dominance ensures feeding priority and subsequent energetic benefit to them. In groups of *Eulemur fulvus*, direct competition over feeding resources is less marked than in other lemur species. In the experimental drinking situation, some individuals obtained priority of access, independently of gender and of social status. Females showed consistent drinking priority in one group, while the male had priority in the other group. From the first minutes of test sessions, individuals taking precedence were able to displace others of either sex from the bottle; they also spent the greatest amount of time in possession of the resource. Relationships between females at the bottle were also different in the two groups. The three females in the two-male group were tolerant of each other, drinking alternately or even simultaneously. On the contrary, in the one-male group, female drinking access was less egalitarian, with one female showing a marked priority.

Broadly similar patterns of intersexual priority of access were revealed in another study on the same groups, confronted with a new feeding task (Anderson *et al.*, 1992). The different composition of the two groups (unimale vs multimale) could account at least partly for the variable priority of access. Thus, in the two-male group, the oldest male spent much time threatening and chasing the second male away from the bottle. To a certain extent, the marked intermale competition elicited by the situation may have favored female drinking priority by diverting male aggression.

Several authors (Jolly, 1984; Kappeler, 1990b) have emphasized that female priority may not be exclusively related to success in agonistic challenges but may result from a non-agonistic spatial deference by males. However, in *Lemur catta,* females supplanted males due to their agonistic success in all contexts including feeding (Kappeler, 1990b; Sauther, 1993). Considering the amount and direction of aggression that we recorded in the competitive drinking situation, the priority of access of some females cannot be explained by male deference. Drinking success is not exclusively correlated with agonistic dominance, while priority of access of some individuals over others can be obtained through aggressive competition. The absence of a correlation for the whole group can be attributed to the different nature of drinking priority between males and females in *E. fulvus*. Female drinking priority in our groups was usually not gained or maintained via aggression but, instead, by resistance in the face of male aggression. Thus, a female could show priority over a male without dominating him aggressively. Infrequently, we observed female aggression with male withdrawal, indicating that females were in fact able to impede male attempts to gain access to the resource. In contrast, male priority was maintained by continuous aggression toward the most competitive females. Data obtained in closely related *Eulemur macaco* (Fornasieri *et al.*, 1993) show that adult females agonistically dominate all other age–sex classes but are frequently challenged by juveniles of both sexes for access to a drinking bottle. Consequently, dominance and drinking success are not correlated in the group; furthermore, they decrease with age in males. Further comparative studies on the emergence and evolution of feeding priority and agonistic dominance are clearly warranted.

A survey of all the studies on lemurid species reveals important inter- and intraspecific variability in social organization, which is echoed by our study. This variability is especially noticeable in agonistic and dominance patterns, for example, between the unambiguous female-dominant species, *Lemur catta* and *Eulemur macaco*, and *E. fulvus*, whose dominance pattern shows no systematic effect of gender. Apart from *L. catta*, true agonistic female dominance with consistent unidirectionality of submissive behaviors has been confirmed only in *Varecia variegata* (Kaufman, 1991) and *Indri indri* (Pollock, 1979). No quantitative datum on the outcome of agonistic episodes has been presented in other prosimian species described as showing female dominance [*Phaner furcifer* (Charles-Dominique and Petter, 1980), *Microcebus murinus* (Perret, 1982); *Propithecus verreauxi* (Richard and Heimbuch, 1975)]. As emphasized by Kappeler (1990b) and Pereira *et al.* (1990), this variability in sympatric and closely related lemur species, which share many aspects of ranging behavior and diet, raises questions about the explanatory adaptative models of female dominance based on energetic costs of reproduction for prosimian females thought to experience particular stress during pregnancy and lactation (Hrdy, 1981; Jolly, 1984). For example, the brown lemur occupies the same biotope as the ringtailed lemur in the south of Madagascar and the black lemur in the north. Moreover, the breeding parameters of these three species are very close (Colquhoun, 1987; Leutenegger, 1979; Richard, 1987). Therefore, it remains unclear why brown lemurs show no female dominance, in contrast to the other two species. As more detailed quantitative data become available on gregarious prosimian groups and agonistic patterns, the original picture of widespread female dominance in Malagasy prosimian primates appears to be misleading.

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