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Female Social Dominance in Semi-Free-Ranging Ruffed Lemurs (*Varecia variegata*)

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Introduction

Although female dominance is a rare trait among mammals [1], it is a striking feature of many lemur social systems [2, 3]. Recent studies of this phenomenon in lemurs have emphasized the importance both of clear documentation of dominance using standard criteria of decided agonistic interactions [4] and of distinguishing between female feeding priority and female social dominance [5]. Female priority and/or female dominance in feeding contexts has been documented in wild studies of *Indri indri* [6], *Propithecus verreauxi* [7], *Phaner furcifer* [8] and captive studies of *Lemur catta* [4, 5], *Eulemur coronatus* [4], *Microcebus murinus* [9], *Daubentonia madagascariensis* [10], and *Varecia variegata* [11]. Female social dominance outside of feeding contexts has been described in *L. catta* [5] and *P. verreauxi* [7]. There is no clear female social dominance in *Eulemur fulvus rufus* [4]. The lack of female dominance in *E. fulvus rufus* has been hypothetically linked to its omnivorous diet and the relatively slower postnatal growth of this species compared to the highly female-dominant *L. catta* [4]. These trends could reduce intersexual feeding competition and the need for intersexual agonistic interactions in this species [4].

The importance of determining whether female dominance in lemurs is more than female feeding priority has important implications for the evolution of this trait [5]. As discussed by Kappeler [5], models that focus on the advantages of female feeding priority in reproductive energetics [2, 12, 13] do not necessarily explain the evolution of female dominance outside of feeding contexts.

This paper presents information on social dominance outside of feeding contexts in captive groups of two subspecies of ruffed lemurs, *V. variegata variegata* and *V. variegata rubra*. This species shows strong female dominance in feeding contexts [11],

Table 1. Subjects and hours of focal sampling

Subspecies	Group	Subject name	Gender	Age[1] years	Living in enclosure[1], years	Residence status	Sampling h	Group total, h
V. variegata rubra	NHE3	EU	F	2	2	founder	10.0	
		NU	F	2	2	founder	10.0	
		DEM	F	1	1	natal	10.0	
		DEN	F	1	1	natal	10.0	
		NO	M	wc 80	3	natal	10.0	
		UR	M	7	3	natal	10.0	
		DO	M	1	1	natal	10.0	70
	NHE6	GAL	F	wc 88	0.5	founder	10.0	
		ALU	F	3	0.5	natal	10.0	
		COM	M	wc 88	0.5	founder	10.0	
		MUR	M	2	0.5	natal	10.0	
		MIR	M	2	0.5	natal	10.0	50
V. variegata variegata	NHE2	BAB	F	17	9	founder	22.8	
		PRA	F	7	7	natal	33.2	
		LET	F	2	2	natal	31.1	
		AMO	M	12	9	natal	31.7	
		CAN	M	23	9	founder	31.7	
		SAR	M	born	born	natal	17.3	
		OCT	M	8	3	immigrant	31.3	
		ZUB	M	8	8	natal	13.0	212

All animals listed are included in focal sampling. wc = Wild caught.
[1]At midpoint of data collection.

as would be expected given its highly defendable and monopolizable frugivorous diet [14–16]. Because it has multiple births [17], it is also expected to have high reproductive energetic demands that would also argue for strong female feeding priority. Female feeding priority may be obtained by female dominance during feeding, male deferral during feeding or other behavioral mechanisms and does not necessarily mean female agonistic dominance. Examinations of intersexual dominance in nonfeeding contexts are needed to determine whether *Varecia* show female social dominance.

Methods

All groups were semi-free-ranging in different enclosures with mixed pine and deciduous forest ranging from 2.3 to 9 ha at the Duke University Primate Center (DUPC). The animals were provisioned each day with monkey chow, fruit or vegetables and water; they supplemented their diet by foraging on natural vegetation [18].

The first group of red ruffed lemurs *(V. variegata rubra)* consisted of 7 related individuals (table 1): the father (NO), 5 full siblings (EU, NU, DEM, DEN, DO) and 1 half-sib from a prior mating of the father (UR). The second group of this subspecies contained a breeding pair (GAL and COM) and their 3 offspring (ALU, MUR, MIR). The group of black-and-white ruffed lemurs *(V. variegata variegata)* consisted of 2 founder animals (CAN and BAB), their 3 mature offspring (PRA,

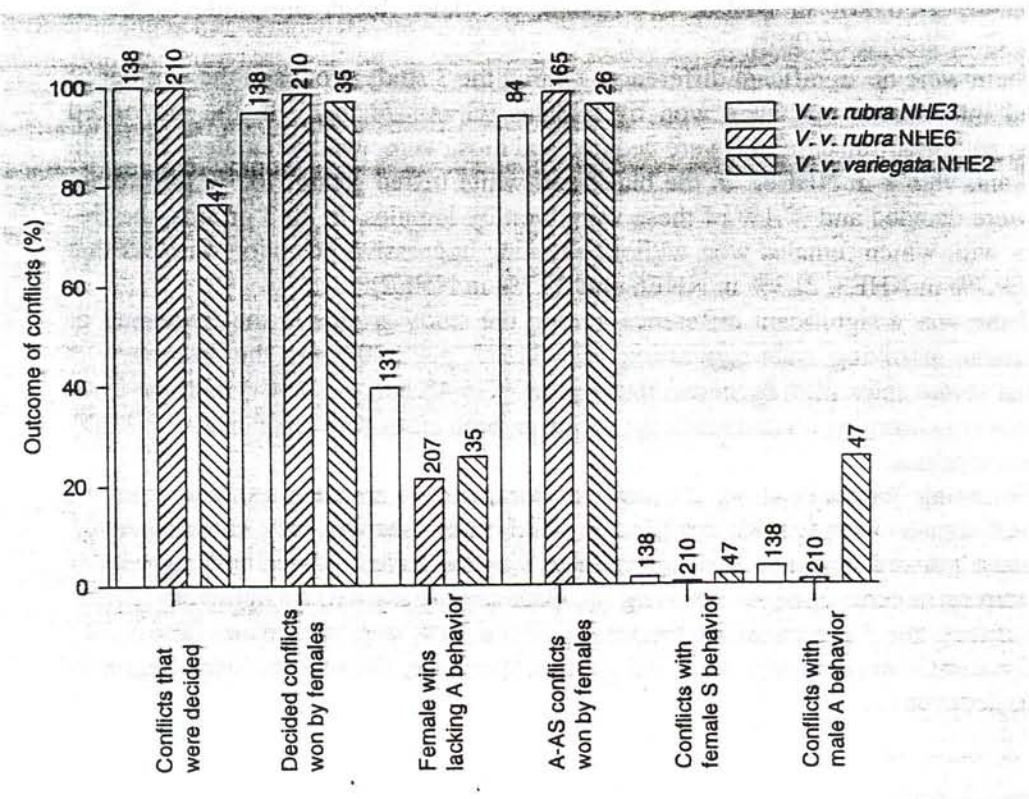

Fig. 1. Six measures of gender effects on agonistic relations between all members of 3 groups of *Varecia*. Bars represent outcomes of intersexual interactions. The total sample size in each category is shown above each bar. A = Aggressive; S = submissive.

AMO, ZUB) and 2 offspring (LET and SAR) of the daughter PRA. This group also contained an immigrant male (OCT) that was a possible father of LET. SAR was probably fathered by ZUB.

Focal animal sampling [19] of nonfeeding individuals was conducted on 2 groups of red ruffed lemurs from September 1992 to April 1993 in the natural habitat enclosure 3 (NHE) and from March 1994 to April 1994 in NHE4, respectively. The black-and-white ruffed lemurs were observed from September 1992 to August 1993 in NHE2. All individuals were identified by uniquely colored collars and tags. Agonistic behaviors were recorded following Pereira et al. [20]. Dominance was defined, following Bernstein [21], as a consistent asymmetry in the outcome of agonistic conflicts between individuals such that the partner which consistently receives submissive signals from and rarely directs them towards the other partner is said to be dominant.

The frequency of interactions was compared using G tests [22] for independence for comparing differences among groups and goodness of fit using expected distributions that assumed no gender-based dominance. Williams corrections were used throughout [22].

Results

In all 3 study groups, females won more decided interactions than expected if both sexes were equally likely to win agonistic interactions (red ruffed in NHE3:

$G = 135.44$, $p < 0.001$; in NHE6: $G = 259.06$, $p < 0.001$; black-and-white ruffed in NHE2: $G = 38.88$, $p < 0.001$).

There were no significant differences among the 3 study groups in the number of decided interactions that were won by females ($G = 0.070$, n.s.). In the red ruffed groups, all intragroup conflicts were decided and most were won by females (94.4% in NHE3 and 98.6% in NHE6). In the black-and-white ruffed group, 76.5% of interactions were decided and 97.1% of these were won by females. In all 3 groups, the frequency with which females won without showing aggressive behavior was less that 40% (39.7% in NHE3, 21.3% in NHE6 and 25.7% in NHE2).

There was a significant difference among the study groups in the frequency of interactions involving male aggression ($G = 31.507$, $p < 0.001$) and the frequency of decided versus undecided agonistic interactions ($G = 45.166$, $p < 0.001$) with the 2 red ruffed groups forming a nonsignificant subset in both cases ($G = 2.836$ and $G = 0.000$, respectively, n.s.).

Following Pereira et al. [4], 2 criteria of dominance were used: a stricter criterion in which females won decided conflicts in which males showed only submissive signals and a 'relaxed' criterion in which females won but males showed both aggressive and submissive behaviors (A–AS in fig. 1). Both criteria showed no significant differences among the 3 groups in the frequency of conflicts won by females ($G = 3.7765$ and $G = 0.0667$, respectively, n.s.). All groups, therefore, showed the same degree of female dominance.

Discussion

Our data demonstrate that ruffed lemurs show unambiguous female social dominance outside of a feeding context. The type and strength of female dominance in this species is similar to that reported for ring-tailed lemurs [4, 5] that were housed in the same enclosure as the study groups of black-and-white ruffed lemurs. In both ruffed and ring-tailed lemurs, most intersexual aggressive interactions were decided and were won by females. Females often won aggressive interactions without showing aggression, females rarely showed submissive behaviors towards males, and males rarely aggressed against females. There were differences between the 2 species in that the ruffed lemur females won fewer interactions without aggressive behaviors than did ring-tailed females (less than 40 vs. over 70% [4]). Ruffed lemurs also showed some male aggression in interactions in addition to some female submission, whereas these behaviors were never seen in the ring-tailed lemurs [4]. This suggests that, although ruffed lemurs are arguably subject to more reproductive and dietary stress than ring-tailed lemurs, their female dominance is somewhat less marked and requires more female aggression to be sustained. These results should be interpreted with caution given the differences in social structure between the species.

Although the 2 subspecies of ruffed lemurs were broadly similar in their pattern of female dominance, there were some differences. The black-and-white ruffed group had more undecided interactions and more interactions that involved male aggression than the 2 red ruffed groups. The 2 red ruffed lemur groups were not significantly different in these categories. The greater frequencies of undecided interactions and male aggression are related, as interactions involving male aggression were mostly undecided. The female showed no response in 11 of the 12 cases of male aggression. In

1 case, the female responded with submissive behaviors to the male aggression. These interactions account for 11 of the 12 cases of undecided interactions. There was 1 case of female aggression with no male response.

Although differences between the ruffed lemur groups may reflect subspecific differences, it is possible that differences in group composition may be responsible for differences in male aggression between the study groups. Only the black-and-white study group contained a recent immigrant male, whereas the red ruffed groups were essentially family groups. However, this recent immigrant was responsible for only 4 out of the 12 agonistic interactions involving male aggression, so this does not appear to be the main factor responsible for these differences. The differences may also reflect seasonal influence in that the data collected for the black-and-white group spanned a year, whereas the data presented here for the red ruffed groups were from September to April and thus did not include the late birth season. However, male aggression in the black-and-white group was distributed throughout the year.

These observations suggest that, although ruffed lemur females are similar to ring-tailed lemur females in being socially dominant, there are differences in the degree of female dominance between the two species and there may be subtle differences between the subspecies of ruffed lemurs.

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