

RESEARCH ARTICLE

Does Female Dominance Facilitate Feeding Priority in Black-and-White Ruffed Lemurs (*Varecia variegata*) in Southeastern Madagascar?

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Although many Malagasy lemurs are thought to be female dominant and to have female feeding priority, to date the relationship between these behaviors has been rigorously established only in *Lemur catta*, and other ways that females might achieve feeding priority have not been examined closely. Erhart and Overdorff [International Journal of Primatology 20:927–940, 1999] suggested that one way female primates achieve feeding priority is to initiate and lead groups to food, thereby gaining access to the food first and positively influencing their food intake compared to other group members. Here we describe female dominance patterns and potential measures of feeding priority in two groups of black-and-white ruffed lemurs (*Varecia variegata*) that were observed over a 15-month period in southeastern Madagascar. We predicted that the females would 1) be consistently dominant to males, 2) lead groups to food sources more often than males, and 3) have higher feeding rates compared to males when they arrived at food sources first. The results were dissimilar between the study groups. During the study, the oldest adult female in group 1 died. There was no evidence for female dominance in this group, and the remaining (likely natal) female did not lead the group more often, nor did she have a higher food intake than males. Group 1 dispersed shortly after the time frame reported here. In contrast, the resident female in group 2 was dominant to group males (based on agonistic interactions), led the group to food sources more often, and experienced a higher food intake when she arrived first at a food source. How these patterns vary over time and are influenced by the number of females in groups, group stability, food quality, and reproductive condition will be examined in future analyses. Am. J. Primatol. 66:7–22, 2005. © 2005 Wiley-Liss, Inc.

Contract grant sponsor: National Science Foundation; Contract grant sponsor: Wenner-Gren Foundation; Contract grant sponsor: University of Texas–Austin.

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Received 16 July 2002; revised 6 November 2003; revision accepted 6 December 2003

DOI 10.1002/ajp.20125

Published online in Wiley InterScience (www.interscience.wiley.com).

Key words: female feeding priority; female dominance; leadership; *Varecia*; Madagascar

INTRODUCTION

Female dominance, which is reported to be a common trait among Malagasy lemurs [van Schaik & Kappeler, 1996], exists when a female consistently receives submissive signals from males but rarely directs submissive signals toward males [Kappeler, 1993; Pereira et al, 1990]. This behavior has been well studied in some species of lemurs and has been observed in a wide range of genera, including *Lemur* [Jolly, 1984; Sauther, 1993; Sauther & Sussman, 1993; Sauther et al., 1999; Taylor, 1986], *Indri* [Pollock, 1979; Powzyk, 1997], *Microcebus* [Radespiel & Zimmerman, 2001], *Varecia* [Morland, 1991a, b], and *Propithecus* [Hemingway, 1999; Kubzdela, 1997; Meyers, 1993; Richard, 1978; Richard & Nicoll, 1987; Wright, 1995; Powzyk, 1997]. *Eulemur* is the one genus in which female dominance is less commonly observed [Overdorff & Erhart, 2001; Pereira & Kappeler, 1997].

Despite the growing documentation regarding female dominance, the benefits of this behavior, particularly during foraging, have not been fully explored. The most widely accepted hypothesis is that female dominance allows females to have feeding priority over males when intragroup contest competition is high, particularly when the females are reproductive [Jolly, 1984, 1998; Kappeler, 1990, 1993; Richard & Nicoll, 1987; Wright, 1999]. Given the presumed energetic costs experienced by lemur females during gestation and lactation [Richard et al., 1991; Young et al., 1990] (but see Kappeler [1996] and Tilden and Oftedal [1997]), female feeding priority, which is achieved through dominance and coordination of group travel to food sources, would have clear advantages. Thus far, this hypothesis has been best supported by work conducted on *L. catta* [Kappeler, 1990; Pereira & Kappeler, 1997; Pereira et al., 1999; Sauther, 1993; Sauther & Sussman, 1993]. *L. catta* females maintain their dominance over males through aggression, lead groups between food sources, and have feeding priority over males [Sauther, 1993; Sauther et al., 1999]. It has been suggested that a leader may have some control over which patches are visited (such as larger, more productive patches or higher-quality foods), which could have an important impact on the health and reproductive success of the leaders [Erhart & Overdorff, 1999].

The black-and-white ruffed lemur (*Varecia variegata*; see Vasey and Tattersall [2002] for nomenclature) is described as female dominant in feeding and social contexts; however, the most quantitative studies on this subject were conducted in captivity [Kaufman, 1991; Raps & White, 1995]. Most studies of wild ruffed lemurs in northeastern [Rigamonti, 1993; Vasey, 1997, 2000, 2002] and southeastern [Balko, 1998; White, 1991] Madagascar focused on other aspects of ecology. To date, the studies conducted in the wild by Morland [1991a, b, 1993] are the only ones that have provided details on dominance patterns for ruffed lemurs. Female dominance, especially during foraging, would be expected from a species that depends on highly defendable and monopolizable fruits and flowers, especially since fruiting and flowering patterns in Madagascar can be highly erratic [Balko, 1998; Rigamonti, 1993; Vasey, 1997, 2000, 2002]. Because female black-and-white ruffed lemurs produce litters and have highly altricial infants [Morland, 1993; Vasey, 1997], they are thought to have high energy demands during reproductive periods, necessitating female feeding priority.

In this study we examined two groups of black-and-white ruffed lemurs to address the following questions: 1) Are females consistently dominant to males? 2) Do dominant females initiate and lead group movements, and as a result arrive at food sources first? 3) Is there a feeding advantage when an individual arrives at a food source before other group members?

MATERIALS AND METHODS

Study Population

This project was part of an ongoing 3-year study comparing patterns of female dominance among three prosimian primates: black-and-white ruffed lemurs (*Varecia variegata*), red-fronted lemurs (*Eulemur fulvus rufus*), and Milne Edward's sifakas (*Propithecus diadema edwardsi*). Two groups of each species are currently being studied at the Ranomafana National Park (RNP) in southeastern Madagascar. RNP is a large (40,000 ha) stretch of rain forest located between 47°18'–47°37' E and 21°02'–21°25' S, and ranges from montane cloud forest (1,500 m) to lowland rain forest (500 m) [Wright, 1992]. The study site, Vatoharanana, is a high montane rain forest (altitude: 1,125 m) with rainfall ranging between 1,500–3,646 mm per year. The predominant plant families in this region are Myrtaceae, Sapotaceae, Rubiaceae, and Lauraceae, and phenological patterns vary somewhat from year to year [Hemingway & Overdorff, 1999]. Nine sympatric species of prosimians are found in the area in addition to the study species.

In this paper we focus on two groups of black-and-white ruffed lemurs that were identified and habituated by the authors during August–December 2000. Data collection began in January 2001. Both study groups contained adult males and females (Tables I and II), and group composition changes were noted throughout the study. Individuals were darted starting in August 2000, following a previously established protocol [Glander et al., 1991, 1992], and were fitted with a uniquely colored collar and pendant for individual identification. In some cases, age or natal status was estimated based on body size and dental development. The data presented here are from January 2001–May 2002, and the groups were sampled for almost equal amounts of time (group 1: 235 hr; group 2: 247 hr). The groups were also sampled equally during reproductive periods (group 1: 121 hr and group 2: 123 hr, July–January) and nonreproductive periods (group 1: 114 hr; group 2: 124 hr, February–June). These time frames overlap the dryer-cooler season (May–November) and warmer-wetter season (December–April), respectively [Hemingway & Overdorff, 1999]. Black-and-white ruffed lemurs show seasonal changes in social organization and feeding ecology at other study sites

TABLE I. Major Demographic Changes in Group 1 Composition from January 2001–May 2002

| Individual/code | Sex | Age class | January 2001 | November 2001 | May 2002 |
|-----------------------------------|--------|-----------|--------------|---------------|------------|
| Radio female (RF1) ^a | Female | Adult | Present | Died | – |
| Red-blue (RB) ^{a,b} | Female | Adult | Present | Present | Present |
| Yellow-green (YG) | Male | Adult | Present | Present | Present |
| Green-blue (GB) ^b | Male | Adult | Present | Present | Present |
| Nocollar male (NCm1) ^c | Male | Adult | Infrequent | Infrequent | Infrequent |

^aNo infants observed at beginning of study, no infants observed in 2001.

^bRB female and GB male observed visiting Group 2 in April 2002, but still considered part of Group 1.

^cUncollared adult male observed visiting group January, March and April 2002, no focal data collected.

TABLE II. Major Demographic Changes in Group 2 Composition from January 2001–May 2002

| Individual/code | Sex | Age class | January 2001 | January 2002 | May 2002 |
|---------------------------------|--------|-----------|--------------|--------------|----------|
| Radio female (RF2) ^a | Female | Adult | Present | Present | Present |
| Yellow-blue (YB) ^b | Female | Adult | Infrequent | Infrequent | – |
| Blue-green (BG) | Male | Adult | Present | Present | Present |
| Red-gold (RG) | Male | Adult | Present | Present | Present |
| Nocollar (NCm2) ^c | Male | Adult | Infrequent | Infrequent | – |

^aNo infants at beginning of study, one infant born in October 2001, disappeared May 2002.

^bYB not sampled and was observed infrequently with group February, June, and November 2001, last seen January 2002 with group.

^cAn uncollared adult male was seen associating irregularly with group members during January, February, October 2001, and January 2002, seen in association with YB Female.

[Morland, 1991b; Vasey, 1997], and our original intention was to examine seasonal differences in dominance, leadership, and feeding patterns. However, at this juncture no seasonal differences have been detected. Consequently, for this analysis, we combined data for the entire 15-month period. Seasonal differences may be more apparent at the conclusion of the full 3-year study.

Female Dominance

We determined female dominance using agonistic behaviors collected during focal animal sampling. One observer conducted focal animal sampling 3 days a week from dawn to dusk for 8–10 hr a day. Each focal animal was followed for a 2-hr interval during which all occurrences of agonistic behavior were recorded. Once a focal animal was sampled, it was not resampled until all other group members were observed, and samples were balanced equally between group members. Because there were infrequent sightings of NCm1 male in group 1 (Table I), and YB female and NCm2 male in group 2 (Table II), these animals were not sampled. However, we noted whether they led the group or interacted agonistically with the focal individual.

The following data were noted during each agonistic bout: the behavior (following ethograms established by Morland [1991b] and Pereira et al. [1988]), the director, the receiver, and the context (resting, traveling, or feeding). Initially, our intention was to record whether an agonistic bout was decided or not (following Pereira and Kappeler [1997]). However, these outcomes were irregularly recorded by different observers. We suggest that this irregularity primarily reflects the fact that the behavioral repertoire of *Varecia* contains few submissive signals. In general, submissive behaviors are used by animals to terminate aggression, and they allow observers to recognize the animal performing a submissive behavior as the “loser,” and the aggressive animal as the “winner” [Bernstein, 1981]. Because we were not able to consistently decide which animals were winners and losers, in this paper we summarize the agonistic bouts in terms of the direction of aggressive and submissive behaviors. We examined the frequency and directionality of aggressive and submissive behaviors to determine whether females consistently directed more aggressive behavior toward males and received more submissive signals from males. G-tests [Sokal & Rohlf, 1995] were used to determine whether individuals within each group directed or received more or less aggression and submission than would be expected by chance. We generated expected values by totaling the number of

times all aggressive behaviors were observed, and dividing that by the number of individuals that interacted.

Leadership Data

While the focal animal sampling was conducted, an additional observer simultaneously collected group movement and leadership data. A leader was defined as an individual that made a “start attempt” within a food source or resting place, and then remained within 5 m of the leading edge of the group (following Boinski [1991]). If the group moved within 10 min of the leader’s movement, the leader’s identity and the order of the remaining group members were noted. The end of a movement was recorded when two-thirds of the group ceased traveling activity for more than 5 min, and the end activity was recorded as feeding or resting. The focal animal observer noted whether or not the leader was the first individual to enter a food source when travel ended. G-tests [Sokal & Rohlf, 1995] were used to determine whether males or females led their groups more often, and whether one sex led more than the other sex when the end activity was feeding.

Diet, Order of Arrival at Food Patches, and Feeding Patterns

We calculated diet, order of arrival at a food source, and feeding patterns using the data collected during focal animal sampling (see Female Dominance section above). In addition to noting all agonistic behaviors of the focal animals, the observer also recorded the following data when a focal animal moved initially into a food source and began to place food in his/her mouth: the focal animal’s order (one, two, or higher), the type of plant part eaten (ripe or unripe fruit, young or mature leaves, and flowers or other food items), and plant species. We determined diet by summing the number of feeding records on each of these plant parts. As the focal animal began to feed, the beginning and end times of a feeding bout (in minutes and seconds) were noted, and the number of bites of food were recorded by a third observer using a hand-held counter.

These data were used to record the number of times each individual in each study group arrived first or second (and higher), and to examine individual differences in feeding bout duration and food consumed per bout (measured in bites). A G-test [Sokal & Rohlf, 1995] was used to determine whether an individual arrived first more often than would be expected by chance, and whether there were individual differences in the total percentage of food consumed when an individual arrived first or later to a food source. For each individual, a Mann-Whitney U-test [Sokal & Rohlf, 1995] was used to test whether order had an effect on feeding bout duration and the number of bites consumed per feeding bout. The significance level was set at $P < 0.05$.

RESULTS

Female Dominance

A total of 295 agonistic bouts were observed, and 258 of these bouts had a clear director and receiver (Tables III and IV). As Pereira et al. [1988] also found, the most common submissive behavior was a chatter vocalization, and the most commonly observed aggressive behaviors were attacks, cuffs, grapples, and chases

TABLE III. Director (DIR) and Receiver (REC) of Aggressive and Submissive Behavior in Group 1 in Nonfeeding and Feeding Contexts*

| DIR/REC | RF (F) | RB (F) | YG (M) | NCm1 (M) | GB (M) | Total nonfeed | Total feed |
|--------------------------------|--------|--------|--------|----------|--------|-----------------|----------------|
| a. Group 1—Aggressive behavior | | | | | | | |
| RF (F) | XXX | 7 (2) | 3 (1) | 0 | 0 | 10 ^a | 3 ^b |
| RB (F) | 0 | XXX | 11 | 8 (3) | 6 | 25 ^a | 3 ^b |
| YG (M) | 0 | 21 (5) | XXX | 3 | 0 | 24 ^a | 5 ^b |
| NCm1 (M) | 0 | 2 | 0 | XXX | 0 | 2 ^a | 0 ^b |
| GB (M) | 0 | 2 | 0 | 1 | XXX | 3 ^a | 0 ^b |
| Total nonfeed ^c | 0 | 32 | 14 | 12 | 6 | | |
| Total feed ^d | 0 | 7 | 1 | 3 | 0 | | |
| b. Group 1—Submissive behavior | | | | | | | |
| RF (F) | XXX | 0 | 0 | 0 | 0 | 0 ^e | 0 ^f |
| RB (F) | 0 (2) | XXX | 1 (3) | 1 | 13 | 15 ^e | 5 ^f |
| YG (M) | 0 | 0 | XXX | 0 | 0 | 0 ^e | 0 ^f |
| NCm1 (M) | 0 | 4 (2) | 3 | XXX | 1 | 8 ^e | 2 ^f |
| GB (M) | 0 (2) | 0 | 0 | 0 | XXX | 0 ^e | 2 ^f |
| Total nonfeed ^g | 0 | 4 | 4 | 1 | 14 | | |
| Total feed ^h | 4 | 2 | 3 | 0 | 0 | | |

*The number of agonistic bouts in feeding contexts is shown in parentheses. Females (F) are listed first, Males (M) are listed second.

^aG=23.31, $P < .0001$, $df=4$.

^bNot significant.

^cG=29.49, $P < .0001$, $df=4$.

^dG=16.80, $P < .002$, $df=4$.

^eG=20.65, $P < 0.0004$, $df=4$.

^fNot significant.

^gG=13.16, $P < 0.01$, $df=4$.

^hNot significant.

(Table V). Agonistic rates did not differ significantly between study groups by context (Fig. 1), and they were higher in nonfeeding contexts when the study groups were combined ($G=17.71$, $df=2$, $P < 0.0001$; Fig. 1).

Certain individuals in each group were more likely to direct and/or receive agonistic behavior than other individuals; however, we were not able to construct linear hierarchies for either group. In addition, not all females consistently dominated all males, and there was variation between females' aggressive and submissive behaviors in groups when more than one female was present. In group 1, which contained two females (RF1 and RB) until November 2001, one female (RF1) never directed submission toward others (Table IIIb) and never received aggression from others in any context (Table IIIa). In contrast, RB female received twice as much aggression in feeding and social contexts compared to others (Table IIIa), and she directed more submission than other group members (Table IIIb). In nonfeeding contexts, RB female and YG male directed the majority of aggression toward each other or NCm1 male (which interacted with the group infrequently).

In group 2, one resident female (RF2) and one female associated infrequently with the group (YB). During feeding, RF2 female was the only individual to direct aggression toward others and to receive submissive signals (Table IVa and b). In nonfeeding contexts, RF2 was responsible for directing 88% ($n=72$) of all aggression, and received 92% ($n=45$) of all submissive behaviors. In particular, RG male directed the majority of submissive signals (92%) toward

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TABLE IV. Director (DIR) and Receiver (REC) of Aggressive and Submissive Behavior in Group 2 in Nonfeeding and Feeding contexts*

| DIR/REC | RF (F) | YB (F) | BG (M) | RG (M) | Total nonfeed | Total feed |
|--------------------------------|--------|--------|--------|--------|------------------|-----------------|
| a. Group 2—Aggressive behavior | | | | | | |
| RF (F) | XXX | 5 | 13 (3) | 54 (7) | 72 ^a | 10 ^b |
| YB (F) | 3 | XXX | 1 | 1 | 5 ^a | 0 ^b |
| BG (M) | 0 | 2 | XXX | 2 | 4 ^a | 0 ^b |
| RG (M) | 0 | 1 | 0 | XXX | 1 ^{a0b} | |
| Total nonfeed ^c | 3 | 8 | 14 | 57 | | |
| Total feed ^d | 0 | 0 | 3 | 7 | | |
| b. Group 2—Submissive behavior | | | | | | |
| RF (F) | XXX | 0 | 0 | 1 | 1 ^e | 0 ^f |
| YB (F) | 1 | XXX | 0 | 0 | 1 ^e | 0 ^f |
| BG (M) | 1 (5) | 1 | XXX | 0 | 2 ^e | 5 ^f |
| RG (M) | 43 (4) | 1 | 1 | XXX | 45 ^e | 4 ^f |
| Total nonfeed ^e | 45 | 2 | 1 | 1 | | |
| Total feed ^h | 9 | 0 | 0 | 0 | | |

*The number of agonistic bouts in feeding contexts is shown in parentheses. Females (F) are listed first, Males (M) are listed second.

^aG=66.23, $P < 0.0001$, $df=3$.

^bG=11.25, $P < 0.01$, $df=3$.

^cG=36.96, $P < 0.0001$, $df=3$.

^dNot significant.

^eG=50.21, $P < 0.0001$, $df=3$.

^fNot significant.

^gG=50.32, $P < 0.0001$, $df=3$.

^hG=10.43, $P < 0.02$, $df=3$.

TABLE V. Agonistic Behaviors (Submissive and Aggressive) Observed

| Group | 1 | 2 |
|------------|-----|-----|
| Submissive | | |
| Chatter | 47 | 74 |
| Avoid | 4 | 0 |
| Flee | 9 | 0 |
| Aggressive | | |
| Attack | 24 | 45 |
| Grapple | 18 | 21 |
| Chase | 3 | 15 |
| Cuff | 10 | 8 |
| Lunge | 6 | 2 |
| Fight | 1 | 6 |
| Bite | 1 | 0 |
| Displace | 1 | 0 |
| Total | 124 | 171 |

RF2 female, and he was also the primary recipient of aggression (Table IVa). When YB female was observed to interact aggressively or submissively with other group members ($n=16$), it was primarily with RF2 female ($n=9$). YB female was the only individual that directed aggression toward RF2 female ($n=3$; Table IVa)

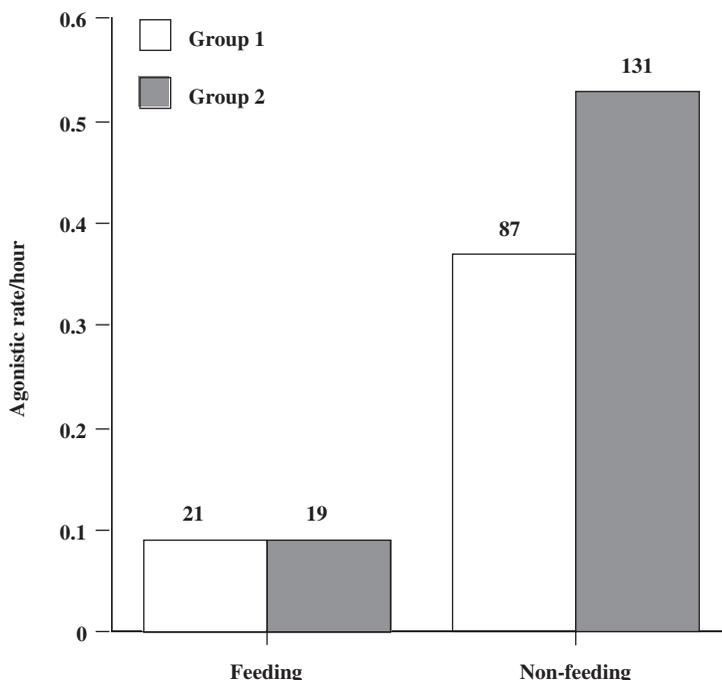


Fig. 1. Rates of agonism per hour by study group for feeding and nonfeeding contexts for Group 1 and 2. Numbers on top of figure bars represent the number of bouts observed.

Leadership Data

A total of 295 group movements were observed in which a distinct leader could be identified (group 1, $n=155$; group 2, $n=140$), and the leader was also the first individual to enter a food source or resting place. Feeding was the end activity of group movements significantly more often than resting for group 1 (feed $n=104$, rest $n=51$, $G=5.99$, $df=1$, $P<0.01$) and group 2 (feed $n=113$, rest $n=32$, $G=16.01$, $df=1$, $P<0.0001$). Although individual differences in leadership patterns were observed, they did not uniformly follow predicted patterns by sex. In group 1, YG male and NCm1 male were more responsible than the females for leading the group to food sources or resting places (feeding $G=11.11$, $df=4$, $P<0.02$; resting $G=14.82$, $P<0.005$, $df=4$; Fig. 2a). In contrast, RF female of group 2 led her group to food sources significantly more often than other group members ($G=37.28$, $df=3$, $P<0.0001$). Both RF2 female and BG male were more likely to lead group 2 to resting places ($G=21.37$, $df=3$, $P<.0001$; Fig. 2b).

Diet, Order of Arrival at Food Patches, and Feeding Patterns

This population was highly frugivorous (group 1: 86%; group 2: 82%) and supplemented its diet with flowers (group 1: 9%; group 2: 10%), leaves (group 1: 5%; group 2: 7.5%), and other foods (group 2: 3%). Because of the small number of observations of other food items, the analyses described below were restricted to fruit sources.

In group 1, although RB female entered fruit sources first slightly more often than any other group member, YG male was the only individual that entered first

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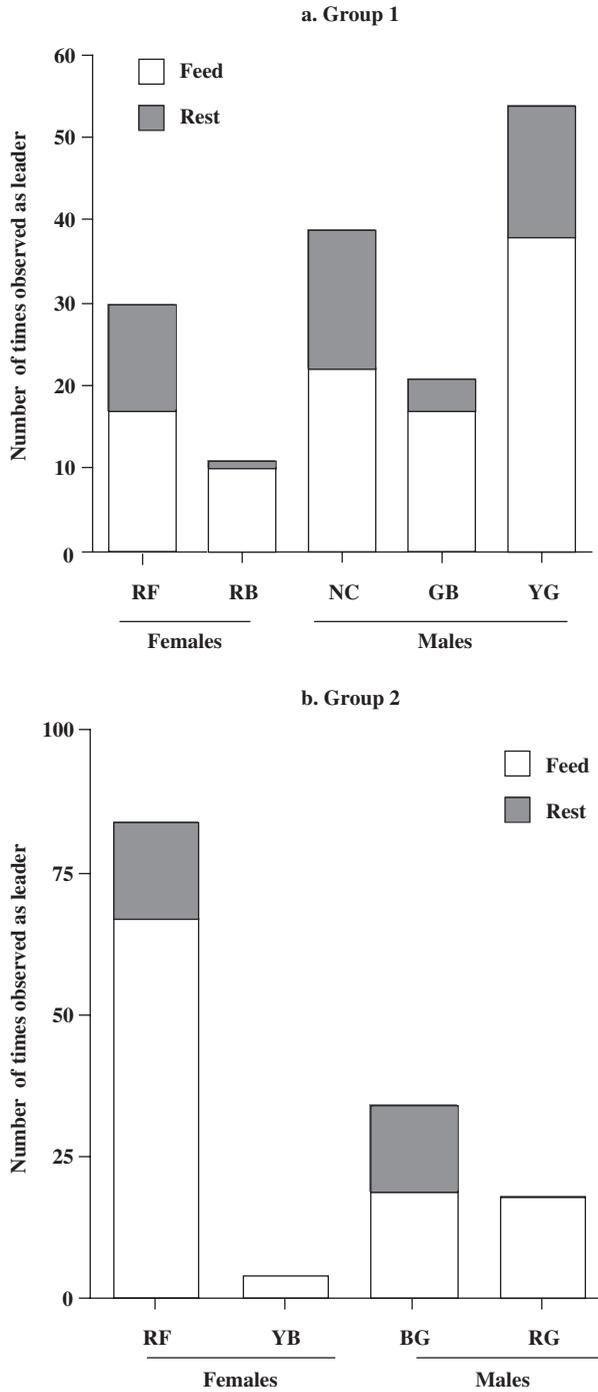


Fig. 2. Number of times each group member was observed to lead a group to a food source or resting place for Group 1(a) and Group 2(b).

more often than would be expected by chance ($G=11.50$, $df=1$, $P<0.001$; Table VI). However, the order of arrival did not influence an individual's bout duration or the number of bites consumed per bout in this group (Table VI). Even though YG male was the only individual to arrive first more often than expected, there were some significant differences in other individuals' percentage of total food intake when order was considered. RF1 female and YG male both consumed the majority of their food during bouts when they were observed to arrive first at a fruit source, while GB male consumed more food during bouts when he arrived second or later (Table VI).

In group 2, RF2 female was the only individual to arrive first at fruit sources more often than expected by chance ($G=24.72$, $df=1$, $P<.0001$; Table VII). She also had a higher number of bites per feeding bout when she arrived first, and consumed more than 80% of her fruit when she arrived first (Table VII). This was not the case for the males in this group; in fact, RG male had longer feeding bouts when he arrived second or later (Table VII), although his order in a fruit patch did not affect the number of bites he consumed.

DISCUSSION

Female dominance and group leadership, and the influence of these two factors on which animal arrived at a fruit source first and whether or not a higher food intake resulted varied by study group in this black-and-white ruffed lemur population. Overall, group 1 did not follow predicted patterns. In group 2, one

TABLE VI. Individual Variation for Group 1 in the Total Number of Times Each Group Member Was Observed to Enter Either First or Later (Second Place or Higher), Mean Feeding Bout Duration in Fruit Sources by Order, Mean Number of Bites per Feeding Bout by Order, and Total Percentage of Food Consumed by Order of Arrival*

| | RF1 female | RB female | GB male | YG male |
|---|--------------|--------------|--------------|---------------|
| Order of arrival | | | | |
| First | 28 | 69 | 22 | 58 |
| Second | 13 | 68 | 23 | 18 |
| G= | 2.82 | 0.01 | 0.01 | 11.50 |
| P= | n.s. (0.09) | n.s. (0.95) | n.s. (0.95) | 0.001 |
| Mean bout duration (min) ^a | | | | |
| First | 9.21 (1.7) | 6.74 (5.5) | 6.88 (4.2) | 6.95 (6.2) |
| Second | 7.52 (1.6) | 6.81 (6.9) | 7.99 (9.9) | 5.45 (4.2) |
| Z= | 0.25 | 0.10 | 0.52 | 0.34 |
| P= | n.s. (0.80) | n.s. (0.92) | n.s. (0.60) | n.s. (0.74) |
| Mean number of bites/ bout ^a | | | | |
| First | 37.61 (6.4) | 30.67 (5.2) | 28.77 (4.4) | 30.72 (5.6) |
| Second | 35.01 (7.1) | 27.25 (5.1) | 61.85 (9.1) | 23.89 (5.3) |
| Z= | 0.03 | 0.87 | 0.27 | 0.37 |
| P= | n.s. (0.97) | n.s. (0.38) | n.s. (0.79) | n.s. (0.71) |
| Total food intake % ^c | | | | |
| First | 69.82 (1055) | 53.31 (2116) | 30.86 (633) | 80.56 (1782) |
| Second | 30.18 (456) | 46.69 (1853) | 69.14 (1418) | 19.44 (430) |
| G= | 8.40 | 0.67 | 7.55 | 21.85 |
| P= | 0.004 | n.s. (0.67) | 0.006 | 0.0001 |

*Degrees of freedom=1 for all tests.

^aStandard deviation in parentheses.

^bTotal number of bites in parentheses.

Bold=significance.

TABLE VII. Individual Variation for Group 2 in the Total Number of Times Each Group Member Was Observed to Enter a Fruit Source Either First or Later (Second Place or Higher), Mean Feeding Bout Duration by Order, Mean Number of Bites per Feeding Bout by Order, and Total Percentage of Food Consumed by Order of Arrival*

| | RF2 female | RG male | BG male |
|--|---------------|--------------|-------------|
| Order of arrival | | | |
| First | 98 | 51 | 41 |
| Second | 24 | 35 | 26 |
| G= | 24.72 | 1.41 | 1.93 |
| P= | 0.0001 | n.s. (0.24) | n.s. (0.16) |
| Mean Bout duration (min) ^a | | | |
| First | 6.62 (0.6) | 6.02 (0.7) | 5.59 (0.8) |
| Second | 6.05 (3.7) | 8.21 (1.8) | 6.88 (1.6) |
| Z= | 0.57 | 2.07 | 1.34 |
| P= | n.s. (0.57) | 0.04 | n.s. (0.18) |
| Mean number of bites/bout ^a | | | |
| First | 42.43 (3.9) | 32.24 (4.0) | 21.63 (3.2) |
| Second | 23.27 (3.9) | 37.78 (3.2) | 38.39 (5.2) |
| Z= | 1.96 | 0.67 | 1.50 |
| P= | 0.05 | n.s. (0.49) | n.s. (0.18) |
| Total food intake % ^b | | | |
| First | 84.57 (3755) | 55.43 (1644) | 47.11 (889) |
| Second | 15.43 (687) | 44.57 (1322) | 52.89 (998) |
| G= | 27.92 | 0.51 | 0.18 |
| P= | 0.0001 | n.s. (0.47) | n.s. (0.67) |

*Degrees of freedom=1 for all tests.

^aStandard deviation in parentheses.

^bTotal number of bites in parentheses.

Bold=significance.

adult female was dominant to the two males in the social group. She led the group more often, arrived first at fruit sources more often, and consumed more fruit per feeding bout when she arrived first. Possible explanations for the variation observed between study groups include differences in group stability and group composition. These differences are discussed in detail below.

Female Dominance

In this study, RF2 female (group 2) was the only female that was clearly dominant to group males. All other male/female dyads exhibited a mixture of aggressive and submissive signals in both study groups. It is important to note, however, that because of the fluidity of the groups, some group members rarely interacted. The social organization of black-and-white ruffed lemurs is extraordinarily flexible, alternately being described as male–female pairs, small multimale–multifemale groups, and communities with up to 31 individuals [Balko, 1998; Pollock, 1979; Morland, 1991a; Ratsimbazafy, 2002; Vasey, 1997; White, 1991]. Overall, black-and-white ruffed lemurs have a dispersed social system and maintain extensive social networks [Morland, 1991a]. For example, RF2 was the only adult female that was consistently present during sampling of group 2, while YB female was only occasionally noted. When they were not with group 2, YB female and NCm2 male were seen traveling and foraging together (Mutschler, personal communication). RF2 female also directed more aggressive behaviors (n=77) toward males compared to YB female (n=2). However, YB

female exchanged aggression more often with RF2 female (YB directed $n=3$; received $n=5$). This result, in conjunction with the infrequent sightings of YB female, suggests that adult female black-and-white ruffed lemurs may not be highly tolerant of each other in this population, and may benefit by preventing other females from joining permanently [Silk, 1983]. Other, well studied ruffed lemur groups in the northeast are larger and are more fluid [Morland, 1993; Vasey, 2000, 2002] compared to the groups described in this paper. Solitary foraging is common in northeastern populations, particularly during gestation, although females show increased gregariousness during lactation when food is abundant and alloparenting would be beneficial. Thus far in this population, permanent group members have not been observed to forage alone for long periods of time (i.e., more than a day), and alloparenting has not yet been documented. As a result, ruffed lemurs may vary widely in group structure and degree of sociality depending on differences in food availability, competition from other species with similar diets, and population density. Further comparisons between populations may elucidate which variables play an important role in shaping the differences observed between populations.

The absence of female dominance seen in group 1 may be due the death of the older female (RF1) and the immaturity of the remaining female (RB). Until her death in November 2001, RF1 appeared to be a dominant female because she directed but never received aggressive behaviors, and she received but never directed submissive behaviors. That statement is somewhat speculative, however, because she died during the study period and thus was not sampled as much as other group members. During the habituation phase of the project in August 2000, we presumed that RB female was a natal female because of her smaller body size (1.5 kg vs. 3.5 kg adult female weight), and that RF1 female was most likely her mother, because there were no other adult females in the group at that time. Although RB female directed as much aggression toward others as did YG male, she was the recipient of aggression far more often than any other individual, and she directed more submissive behaviors toward others. Clearly she was not a dominant female. Therefore, the ability of a black-and-white ruffed lemur female to be dominant over others in her group may depend on age and group stability. In captive populations a maturing daughter will either oust her mother from a social group and establish dominance over other group members, or transfer to a new group and possibly improve her dominance status [White et al., 1992]. RB female's behavior in group 1 may be an example of a similar pattern. The destabilization of group 1 continued after the study period ended, and apparently resulted in the splitting of the group. Between May and September 2002, RB female and GB male were observed occasionally with group 2. In March 2003, it was reported that group 1 members could no longer be located together, and YG and BG males were seen in association with YB female from group 2 (Mutschler, personal communication). Future work may elucidate whether the presence of an older, socially established female is required to maintain a stable social group in this species.

In sum, based on the variability within and between study groups, this population cannot be conclusively labeled "female dominant." This is consistent with a growing body of evidence showing that while many prosimian females commonly direct agonism toward males, unchanging linear hierarchies (as seen among anthropoids) are rare, not all females are dominant to all males in many species, and *L. catta* may in fact be the only Malagasy prosimian species to demonstrate true female dominance [Hemingway, 1999; Kappeler, 1990; Kaufman, 1996; Morland, 1991b; Pereira & Kappeler, 1997; Pereira et al., 1999;

Sauther, 1993; Sauther & Sussman, 1993; Sauther et al., 1999]. Indeed, Raps and White [1996] suggested that in comparison with *L. catta*, female dominance in black-and-white ruffed lemurs is not as clear-cut and requires more female aggression to be sustained.

Leadership and Order of Arrival at Fruit Sources

Originally we suggested that leadership of a group, particularly to fruit sources, could be linked to female dominance and/or age and tenure of group members. In group 2, the dominant female consistently led the group to fruit sources, entered feeding trees before other group members, and had a higher bite count per bout when she arrived first compared to when she arrived after other group members. Erhart and Overdorff [1999] noted similar patterns in sifaka (*Propithecus diadema edwardsi*) and brown lemurs (*Eulemur fulvus rufus*). By initiating and leading group movements, the leader may have some control over which patches are visited (e.g., larger, more productive ones), and leaders may increase their chances of arriving first at a food source. This could be considered a form of female feeding priority because RF2 female (group 2) had a higher food intake per bout when she arrived first, even though the overall feeding bout durations were the same for all individuals. She may have consumed more food per minute of feeding because by arriving first she had first pick of the available foods that had not yet been depleted by other group members, and she may have been less likely to be interrupted by other group members. As with *L. catta* [Sauther, 1993], female feeding priority in this form may be maintained primarily through female aggression since RF2 female was typically the individual that directed aggression toward others in feeding and nonfeeding contexts. However, in group 1, YG male often led groups to fruit sources, but did not show differences in bite count or bout duration when he entered first or later (Table VI). Although YG male consumed a higher percentage of his total food intake when he entered a feeding tree first, so did RF1 female, who did not lead the group very often.

Variation in leadership between groups may be related to differences in food quality or the reproductive stage of the adult female. Individuals in group 1 may have exploited higher-quality resources overall, and thus arrival at fruit sources first would not necessarily offer any advantage. This issue will be explored in future analyses of the nutritional quality of food. Reproductive females may have higher energy requirements throughout the year [Vasey, 2000, 2002] (Vasey, this volume). This may select for female dominance to maintain feeding priority, and influence whether females lead groups to food sources and reap the potential nutritive benefits of arriving first. For example, RF2 female was observed building nests in 2000, 2001, and 2002, while RB female was never seen to build a nest. It is also possible that a similar pattern in dominance, leadership, and influence of order of arrival on food intake would have been observed in group 1 if RF1 female had not died. Another factor to consider is the role that age and/or tenure may play in group leadership. Based on age estimates at the time of capture, YG male (group 1) and RF2 female (group 2) were the oldest individuals in their respective groups. Older individuals in social groups may have greater knowledge of the location of food sources, and their phenology and temporal distribution, and therefore would be more likely to lead groups [Rowell, 1969]. In sum, given the variability between study groups, the results are still inconclusive as regards the importance of leadership and first arrival at a resource in this species.

We conclude that black-and-white ruffed lemurs in this population cannot be considered to be definitively female dominant based on the variation between study groups. While one group (group 2) demonstrated that an adult female can be dominant to males, dominance relations were unclear in group 1. Additionally, the influence of order of arrival at fruit sources on food intake varied between study groups. Future work will attempt to clarify the role that group stability, age, reproductive status, and influence of food quality have on leadership, female dominance, and female feeding priority.

ACKNOWLEDGMENTS

D.J.O. and E.M.E. thank Thomas Mutschler for his hard work in keeping the project going under difficult circumstances. We also thank Fidy Ralainasolo, Hubert Andriamaharoa, Clayton Clement, Albert Telo, Victor Rasendrinirna, Zafi Razafindravelo, Koto Rakotoniriana, Michel Rakotoniriana, Fano Rafanomezatsoa, and Aimée Razafiarimalala for their support and insight while this project was conducted in Madagascar. The following are acknowledged for facilitating the success of this project in Madagascar: Benjamin Andriamihaja, Patricia Wright, MICET, ANGAP, and ICTE. We also thank Laura Alport, Steig Johnson, Christina Grassi, Rebecca Lewis, Joyce Parga, three anonymous reviewers, Michael Andrews, and Natalie Vasey for helpful comments on the manuscript. This paper is dedicated to the memory of A. Wolfe and J. Overdorff.

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