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SOCIAL ORGANIZATION, FEEDING ECOLOGY, AND REPRODUCTIVE STRATEGY OF RUFFED LEMURS,
VARECIA VARIEGATA

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The social organization of ruffed lemurs is variable. Original descriptions of monogamous social structure in the wild [1,2] were confirmed by observations of captive animals in outdoor runs [3-7]. It became clear, however, when ruffed lemurs were moved into a large natural habitat enclosure at the Duke University Primate Center (DUPC), that social behavior was very changeable [8]. The intolerance between mothers and mature daughters, characteristic in smaller cages [7], was dramatically reduced so that both mothers and daughters bred in the group, and larger group sizes became possible [9-11]. Observations in Madagascar of groups derived from introduced animals [12] have also reported larger group sizes. When larger groups became possible at DUPC, however, ruffed lemurs did not form cohesive groups [8-10,13]. These observations lead to suggestions that ruffed lemurs may show a fission-fusion social organization similar to that of chimpanzees and spidermonkeys [10].

Ruffed lemurs, as well as displaying unusual social variability, have a unique reproductive strategy. Unlike other medium-sized diurnal primates, ruffed lemurs give birth to litters rather than single offspring, build nests exclusively for the care of these infants, and carry their infants in their mouths [2,7,9,10]. This deviation from the intensive maternal care of a single offspring more characteristic of larger diurnal primates, provides an opportunity to study the evolutionary significance of maternal care and single births in primates.

This paper presents data on the social organization and ecology of ruffed lemurs from observations of wild animals in undisturbed natural rain forest of southeastern Madagascar and from studies of free-ranging groups at DUPC. These observations are used to generate hypotheses on the evolution of ruffed lemur reproductive strategy.

METHODS

1. Wild studies. Ruffed lemurs were observed for 112 hours over two months at Vatoharanana in the proposed Ranomafana National Park in southeastern Madagascar. The study site is undisturbed, continuous rain forest at 1100m elevation. Ruffed lemurs are sympatric with 11 other lemurs and potential aerial and terrestrial predators including *Cryptoprocta ferox*. The lemurs at Ranomafana have historically never been hunted. A study group was located and a mapped trail system of 3.5 km² was started. Individuals were recognizable from differences in pelage. The study group has been censused by researchers (D. Overdorff, C. Hemingway) at the site until June 1990.

2. Free-ranging studies. The first matriline of ruffed lemurs at the Duke University Primate Center were established in 1962. All individuals are identified by colored collars and pendants. A social group of ruffed lemurs has been maintained in free-ranging conditions in natural forest habitat enclosures (from 1983 to 1985 in a 0.59 ha, since 1985 in a 3.30 ha enclosure, areas from Balko, pers. comm.). A second group was released into a neighboring 5.83 ha enclosure in 1988 (Balko, pers. comm.). The study group consists of an adult female, an adult male, and offspring.

RESULTS

1) Wild studies. The study group consisted of an adult male and an adult female [13]. Only one subadult was observed within the pair's territory. This lemur exchanged calls with, but did not associate with, the cohesive pair. The pair maintained a very large territory (197 ha), and frequently ranged more than 1 km each day. The male and female used chorusing loud calls for territorial behavior at the boundaries and for coordination of movement within the territory. Loud calls were usually given before the pair traveled long distances. Movement by the pair was coordinated but not cohesive, and they often slept in separate

trees. The pair did not vocalize usually after arriving at a food tree. The territory was surrounded by the territories of, on one side, a group of three (Overdorff, pers. comm.) and, on two sides, pairs of ruffed lemurs. The study pair, most recently observed in May and June 1990, is still together in the same territory (Overdorff and Hemingway, pers. comm.).

Most of the food patches visited by the ruffed lemurs at Vatoharanana were fruit trees and the ruffed lemurs supplemented their diet with small amounts of nectar and leaves (Table 1). Day ranges varied from 2250m to 750m, with an average of 1129m (n=12). The ruffed lemurs fed, traveled, and rested mostly high in the continuous canopy (20 to 25 m), although they occasionally came to the ground to eat soil.

TABLE 1. FOOD PATCHES USED

Food Type	Frequency	Percent
Fruit	51	70.8
Leaves	8	11.1
Flowers*	2	2.8
Nectar	11	15.3

* flowers were licked
and not eaten

TABLE 2. DISTRIBUTION OF TREE SIZE FOR FOOD TREES AND IN A 50X50M QUADRAT

DBH (cm)	food trees percent	quadrat percent
3-20	5.5	84.5
21-40	24.7	7.9
41-60	24.7	4.8
61-80	32.9	1.6
81-100	4.1	0.8
>100	8.2	0.0

Ruffed lemurs used mostly large food trees (mean radius of 7.2m, mean dbh of 52.1cm, n=40). The density of food patches at the study site was estimated from measurements of trees in a 50x50m quadrat. The diameter at breast height (dbh) is used here as a measure of size as there was a significant linear regression of dbh on radius of the food trees used at Vatoharanana (radius = $4.42 + [0.053 \pm 0.0121] \text{dbh}$, $F=19.09$, $p<0.001$, $R^2=33.4\%$). The large trees used by ruffed lemurs occur at relatively low densities in the forest (Table 2).

2) Free-ranging studies. At DUPC, the level and type of cohesion among individuals in the free-ranging group varied with the sexual cycle and age of individuals. At the onset of the breeding season, there was an increase in cohesion among the individuals (Table 3). The group was not cohesive and it was rare to observe all individuals together in one place (Table 4).

TABLE 3. NUMBER OF VARECIA IN COHESIVE UNIT (WITHIN 15 METERS)

Group size:	1 - 3 (%)	4 or more (%)
before Oct 25	61	39
after Oct 25	44	56

(Total 7 individuals; data collection by L. Alvarado-Benson. Sexual cycles begin in mid-November)

TABLE 4. PERCENT OF TIME SPENT IN ASSOCIATION (WITHIN 5M) OF OTHERS

Number of neighbors	Percent of time
0	38
1	26
2	14
3	14
4	8

(Total 5 individuals in group; data collection by G. Kratt, M. Nix, P. Gaynor, K. Karavanich, Sept-Dec '89)

Cohesion varied with the age of individuals. Young adolescent males showed little cohesion or coordination with other group members and are the most likely to actively disperse without aggressive eviction by other group members. Adult breeding females also disperse, but they are aggressively evicted from social groups by higher ranking females.

DISCUSSION

The pattern of cohesion observed in the natural habitat enclosures is not consistent with a fission-fusion social organization as individuals are not organized into cohesive parties and dispersal and evictions result in there being

only one long-term resident successfully breeding male and female in the group. At DUPC, it is often the maturing daughter that becomes the breeding female. Daughters born to captive ruffed lemurs at the Duke University Primate Center are usually removed at the time of the daughter's first estrus because this is a time of rapid escalation of aggression in the group [7]. Of 110 offspring (61 female and 49 male) born at the Duke University Primate Center since 1962, the dominance status is known for 22 females. Before individuals were removed from groups for management purposes, 45% of female offspring outranked their mothers.

When captive ruffed lemurs were moved to large enclosures, the dynamics of the mother-daughter interactions were clearly observed [11]. When the ruffed lemurs were first moved to the large outdoor natural habitat enclosure, a daughter was able to remain in the group past her first estrus. This daughter remained in the group for the next two years. During this time, she mated with her father and gave birth, unsuccessfully, to two sets of offspring. Although the daughter and mother interacted affiliatively, aggressive interactions showed that the daughter clearly outranked the mother. Following the daughter's third breeding season with her father and subsequent successful birth, all affiliation between the females ceased and the daughter aggressively evicted the mother from the social group. The mother then attempted to disperse by traversing the electric fence bounding the enclosure, and was later recaptured. The daughter and offspring were removed from the group and the mother reintroduced for management purposes. This situation is now being repeated with the same mother and a second maturing daughter in the group. The daughter has mated and bred successfully and presently outranks the mother.

The observations of wild animals, however, show a type of monogamy that parallels the social system observed for gibbons [14-16]. The coordination but relative loose cohesion between the male and female, to the extent of traveling and feeding dispersed, the chorusing behavior, and territorial defense are behaviors typical of gibbons [15,16].

Under natural conditions, therefore, ruffed lemurs can be monogamous. In captivity, both male and female offspring are unable to disperse and remain with their natal group longer. In Madagascar, *Varecia* groups introduced onto the small island of Nosy Mangabe [12] and in isolated forest blocks such as Kanjavato (Keith-Lucas, Ryan, pers. comm.) have small home ranges and large group sizes. This variation may be a consequence of limited dispersal. Variations in social strategy may also reflect altitudinal differences, with larger groups in lowland forest to monogamous pairs in montane forest.

Reproductive strategy. Ruffed lemurs at Vatoharanana traveled extremely long distances, for a 3 to 4 kg animal, each day to visit scattered food sources and to defend a large territory. The energy demands of this traveling must be great. Unlike most primates, ruffed lemurs do not carry their offspring continuously, but instead park the infants in nests. Carrying of infants is expensive, especially as it occurs when females are energetically stressed from the demands of lactation in the highly seasonal environment of Madagascar. Carrying is a non-shareable parental investment [17], i.e. if one infant is carried, there is less energy available to carry a second, or third, offspring. If energy for reproduction is limited, and non-shareable care is essential for infant survival, the number of infants that can be supported may be limited [17]. If females do not rely on such non-shareable care, however, but instead use a shareable form of parental care like infant guarding, this possible limiting factor to the number of offspring may be removed, making it possible to have and nurse several infants at a time. Predation may also play a factor in selection for litter size, as presumably infants are more vulnerable when left in nests than when carried by adults. This does not explain why other primates do not also have litters and not carry their offspring. The crucial factor for ruffed lemurs may be the need to travel large distances between scattered fruit trees in order to make a living as a frugivore in a highly seasonal environment such as Madagascar.

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