

Population Demography and Social Structure Changes in *Eulemur fulvus rufus* From 1988 to 2003

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ABSTRACT *Eulemur fulvus rufus* has been described as having stable multi-male/multi-female groups, a male-biased sex ratio, and female philopatry. However, in a 16-year study of this subspecies we documented a great deal of demographic change as several groups permanently fissioned, some groups disappeared, and new groups formed. We split the dataset into two periods, 1988 to 1993 and 1994 to 2003, which coincided with the first disappearance of a study group (in August 1994) and the first permanent group fission (in December 1994). The average group size decreased by nearly half between the study periods (10.5–5.6), while the frequency of group membership changes increased (2.0–8.3 times/year), and the birth rate decreased (0.56–0.38). Females, as well as males, immigrated into study groups and transferred

between groups, something that has been rarely seen in this subspecies. We also found a significant decline in the amount of fruit from the earliest part of the study to the latter part of the study. Study groups did not switch to other types of foods during periods of fruit shortage, but traveled outside of their home range areas more often over the study period. Finally, the density *E. f. rufus* decreased in the study area while the densities of their main food competitors, *Varecia variegata* and *Eulemur rubriventer*, increased. Although few primate populations are numerically stable over time, we suggest that female behavioral responses to decreases in fruit availability may have influenced some of the demographic changes we witnessed in this study. *Am J Phys Anthropol* 136:183–193, 2008. ©2008 Wiley-Liss, Inc.

To better understand primate demographic patterns, researchers need longitudinal data on factors such as developmental patterns, reproductive rates, emigration, and immigration events, and differential mortality by age and sex. Long-term studies are particularly critical for primates because of their relatively long lifespans, delayed maturation and slow reproductive rates (Charnov and Berrigan, 1993), and because groups and populations are not stable over time but experience a constant state of flux due to births, deaths, migrations, and maturations (Rowell, 1967; Altmann and Altmann, 1979; Dunbar, 1979; Mueller et al., 1991; Cowlshaw and Dunbar, 2000; Lee and Kappeler, 2003; Strier, 2003; Jones, 2005). These latter processes can alter features of social structure such as the adult sex ratio, group size and group composition in relatively short periods of time, and are tied to ecological and nonecological conditions. Ecological conditions include resource distribution and predation risk and have been well studied since the 1960s (Crook and Gartlan, 1966; van Schaik, 1983; Terborgh and Janson, 1986; Wrangham, 1987; Standen and Foley, 1989; van Schaik, 1989; Janson, 1998; Pereira et al., 1999; Janson, 2003), while our understanding of nonecological conditions, such as reproductive strategies and sexual conflict, has improved recently (Dunbar, 1979; Clutton-Brock, 1988; Dunbar, 1995; van Schaik, 1996; Pusey et al., 1997; Kappeler, 1999; van Schaik et al., 1999; Davies, 2000). Behavioral responses to local demographic conditions are thought to be highly flexible or plastic, and operate on a shorter temporal timescale compared to physiological and morphological responses (Strier, 2003; Jones, 2005).

Detailed data are now available on the demography of a range of wild anthropoids from the Old and New Worlds (*Theropithecus gelada*: Dunbar, 1980; *Papio cyno-*

cephalus: Altmann et al., 1985; Alberts and Altmann, 2003; *Pan troglodytes*: Sugiyama, 1994; Nishida et al., 2003; *Macaca fuscata*: Takahata et al., 1998; *Macaca fascicularis*: van Noordwijk and van Schaik, 1999; *Presbytis thomasi*: Wich et al., 2007; *Alouatta palliata*: Froelich et al., 1981; *Alouatta caraya*: Rumiz, 1990; *Alouatta pigra*: van Belle and Estrada, 2006; *Brachyteles hypoxanthus*: Strier et al., 2006), although little is known about the demography of prosimian taxa. Current information regarding lemuroid demography is based primarily on four species representing three genera (*Lemur catta*: Sussman, 1991; Jolly et al., 2002; Gould et al., 2003; *Propithecus verreauxi*: Richard et al., 1991; Richard et al., 2002; *Propithecus edwardsi*: Wright, 1995; Pochron et al., 2004; *Eulemur fulvus rufus*: Overdorff et al., 1999).

Based on a long-term study (1988–1998) of the social structure of *Eulemur fulvus rufus* (red-fronted brown lemur) at the Vatoharanana study site in the Ranomafana National Park, Overdorff et al. (1999) described this subspecies as having stable multi-male/multi-female

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groups with an average of 9.5 group members, a male-biased sex ratio and female philopatry. These results are consistent with reports from other eastern and western populations *E. f. rufus* (Sussman, 1974; Gerson, 2000). Continued study of *E. f. rufus* at the Vatoharanana study site, however, suggests that the demographic profile and social structure of this subspecies may be more flexible than originally reported. In this study we describe changes from July 1988 to August 2003 in basic demographic variables such as average group size, adult sex ratio, birth patterns, immigrations and transfers of adults between groups, short-term group migrations, permanent group fissions, disappearances of individuals and groups from the study area, and population density. We attempt to relate changes in these variables to changes in ecological conditions over this nearly 16-year period and consider these changes in terms of the conservation management of this subspecies. Although *E. f. rufus* is currently classified in the "lower risk" category by conservationists, it was recently downgraded from the sub-category "least concern" to "near threatened" (IUCN, 2000). This means that *E. f. rufus* is close to qualifying for, or likely to become, "vulnerable" in the near future. More specifically, after studying the interactions between social structure, demography and gene flow of *E. f. rufus* at Vatoharanana, Merenlender (1993) suggested that this population may not be self-sustaining.

METHODS

Study site

Ranomafana National Park was established in 1991 and encompasses 43,500 ha (21° 16'S, 47° 20'E) of submontane rainforest in southeastern Madagascar. Although the forest of Vatoharanana underwent selective logging from 1987 to 1988, overall it has experienced little human disturbance (White et al., 1995; Balko, 1998). Monimiaceae, Cunoniaceae, Lauraceae, and Myrtaceae are predominant plant families (Schatz and Malcomber, 1993). In terms of fauna, there are 11 primate species in addition to *E. f. rufus* in the Ranomafana National Park (Wright, 1992), and several predators of large-bodied lemurs exist there including *Cryptoprocta ferox* (fossa), *Polyboroides radiata* (Madagascar harrier hawk), and *Accipiter henstii* (Henstii's goshawk) (Wright, 1998; Karpanty and Wright, 2007). At the study site, cooler, drier months occur between June and September (rainfall < 150 mm/month, range 4–20°C) and warmer, wetter months fall between October and March (rainfall > 150 mm/month, range 11–31°C).

Study species

In this study we used demographic data from a total of six *E. f. rufus* groups that were sampled from July 1988 to August 2003 at the Vatoharanana study site in the Ranomafana National Park. Groups were studied almost continuously as parts of long-term studies (see Overdorff et al., 1999, 2005 for details); during breaks between these long-term studies groups were monitored during monthly censuses (Johnson and Overdorff, 1999). We split the data into two periods, 1988 to 1993 and 1994 to 2003, which coincided with the first disappearance of a study group in August 1994 and the first permanent group fission in December 1994.

Group composition

Group size, births, sex ratios, disappearance of individuals, emigrations, immigrations, transfers, group fissions, group migrations, and group disappearances were noted for *E. f. rufus* throughout the study period. Although group size data does not include infants less than 6 months of age, all infants born during the study period were used to calculate birth intervals, birth rates, and infant sex ratios at birth. All adult study subjects were individually recognizable by collars and pendants, and one individual in each study group wore a radio collar to facilitate location of study groups (see Glander et al., 1991 for methods). Dated individuals were weighed and standard morphometric measurements were collected (see Glander et al., 1992 for methods). An individual's age was determined based on known date of birth or was estimated based on the degree of tooth wear (Strait and Overdorff, unpub. data). "Infant" refers to animals less than 1 year of age and "juvenile" refers to animals between 1 and 2 years of age. Because this subspecies is sexually dichromatic, infants were discernable as male or female shortly after birth. Overdorff et al. (1999) found that the orange tuft on top of the head of adult males is present in infant males within a week of birth. Migrants under the age of 3 years have not been observed for this species. Therefore, infants and juveniles that disappeared during the study period are categorized as "dead." Finally, "adult" refers to animals aged 2 years or older. Females give birth for the first time between 2 and 4 years of age; the minimum body weight necessary for successful pregnancy is ~2.3 kg (Overdorff et al., 1999).

Ecological factors

Phenological sampling was conducted monthly from August 1988 to August 2003 to estimate seasonal food availability. From 1988 to 2000 data come from four 5 m × 50 m transects (see Overdorff et al., 1999 for details), while from 2001 to 2003 a 50 m × 100 m botanical plot was established. Although the total number of trees differed between the types of sampling methods (transects = 271 trees; botanical plot = 401 trees), the proportion of trees bearing fruit each month did not (transects mean = 8.4, std dev = 2.4; botanical plot mean = 7.6, std dev = 2.9; Wilcoxon Signed Rank Test $Z = -1.01$, $P = 0.31$). Therefore, we were able to calculate the proportion of trees bearing fruit within the transects and the botplot for each month of the study period to document changes in abundance from year to year and during different reproductive phases. These data were compared monthly using a Wilcoxon's Signed Ranks Test.

Rainfall was noted daily throughout the study and averaged for each study year (Overdorff and Wright, unpub. data; Overdorff and Erhart, unpub. data). Because Madagascar is in the cyclone belt (10°–20° S), cyclones and tropical storms occur regularly in southeastern rainforests during the months of February to March. Tropical storms have maximum wind speeds of 60–90 km/hr, while cyclones have wind speeds exceeding 90 km/hr and often reach 160 km/hr or higher (Donque, 1972). Because cyclones and tropical storms can have a devastating impact on habitats, this kind of activity was also noted.

Population density

Eastern *E. f. rufus* is highly frugivorous, with fruit making up at least 50% of the monthly diet (Overdorff,

1993). Therefore, census data on the other sympatric, gregarious frugivores were collected to compare population densities. Data on *E. rubriventer*, *Varecia variegata*, and *P. edwardsi* were collected during monthly censuses from July 1988 to August 2003. Populations of *E. f. rufus*, *E. rubriventer*, *V. variegata*, and *P. edwardsi* were estimated using transect methods (Cant, 1978; Brockelman and Ali, 1987; Whitesides et al., 1988). Because we wanted to limit habitat damage due to cutting straight line transects, we used the existing trail system, which traversed various microhabitats and altitudes. We surveyed 18 transects total, transects varied in length from 250–1,200 m and each transect was walked on a predetermined day once per month. Densities were calculated by dividing the number of individuals observed by the total survey area. Survey area was obtained by multiplying total survey length by transect width. Transect width was determined by using the estimated perpendicular distance from a group to a transect along with the histogram inspection technique, with a 50% criterion for falloff distance (Whitesides et al., 1988).

TABLE 1. The population structure of *E. f. rufus* from July 1988 to August 2003

	1988–1993 ^a	1994–2003
Average group size ^b (std dev)	10.5 (2.8)	5.6 (1.6)
Average number of adult males in groups (std dev)	5.5 (2.1)	3.3 (0.91)
Average number of adult females in groups (std dev)	3.1 (0.80)	2.1 (1.0)
Adult M:F ratio	1.73 (71:41)	1.56 (50:32)
Average number of juveniles in groups (std dev)	1.7 (0.76)	2.1 (1.0)
Number of infants born in groups ^c (number disappeared ^d)	19 (8)	13 (3)
Infant M:F ratio ^c	2.17 (13:6)	0.86 (6:7)

^a These data are from Overdorff et al., 1999.
^b Group size did not include infants less than six months of age.
^c Includes all infants born into groups.
^d These infants were assumed to have died.

RESULTS

Group size and adult sex ratio

Mean group size for *E. f. rufus* decreased from 1988 to 2003 (Table 1, Fig. 1). Study groups averaged 10.5 individuals (± 2.8) from 1988 to 1993, but decreased to an average of 5.6 individuals (± 1.6) during 1994 to 2003. There were 30% fewer males and 22% fewer females in groups in the latter period (Table 1). This drop in the number of males resulted in a slight decline in the male:female sex ratio from 1.73 from 1988 to 1993 to 1.56 during 1994–2003 (Table 1, Fig. 2).

Birth patterns

Not only were there fewer females in study groups over time, fewer females reproduced each year (1988–1993: $n = 19$, range = 0–6 females, mean = 3.2, std dev = 2.2; 1994–2002: $n = 15$, range = 0–3 females, mean = 1.7, std dev = 1.5). In addition, most females (88%) gave birth in consecutive years during 1988 to 1993 (although not all infants survived); however, this figure dropped to 62% during 1994 to 2002 as most females gave birth every other year. This difference is illustrated in the average interbirth interval for surviving infants, which was 1.6 years ($n = 10$, std dev = 2.3, range = 1–3) during 1988 to 1993, but was 2.1 years ($n = 10$, std dev = 3.2, range = 1–3) during 1994 to 2002.

Infant mortality was 42% (19 infants born, 8 died) for *E. fulvus rufus* from 1988 to 1993 (Table 1), and female infants suffered higher mortality rates than male infants. In contrast, fewer infants were born between 1994 and 2003 ($n = 13$), but the infant mortality rate was only 23% and two of the three infants that died during this period were males. Finally, there was a decline in the infant sex ratio between the two study periods with fewer males born in the latter period (Table 1).

Our greatest longitudinal data on infant births and first year survival come from Group 1. To calculate the birth rate for Group 1 we divided the number of infants born by the number of reproductive females for each year from 1988 to 2002 (Table 2). Overall, we found a decrease in the birth rate (the proportion of females that

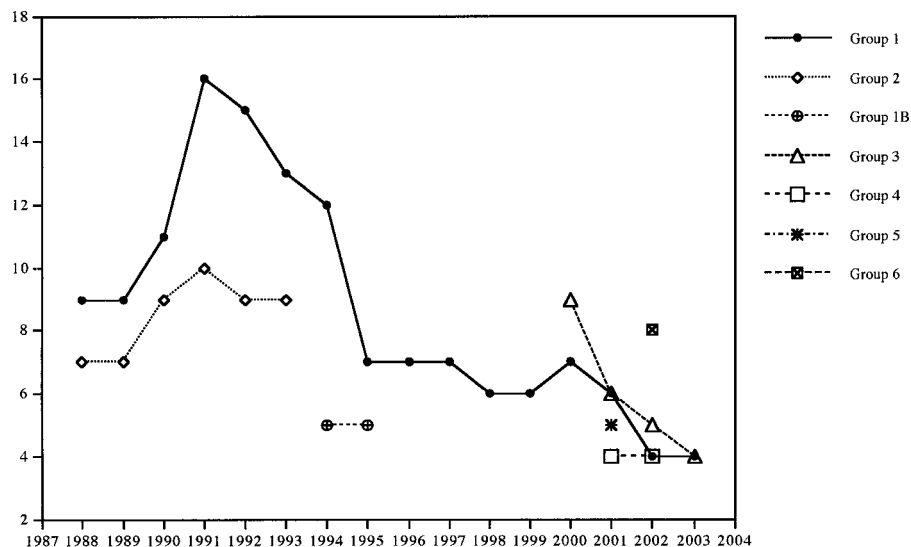


Fig. 1. Mean group size changes from July 1988 to August 2003.

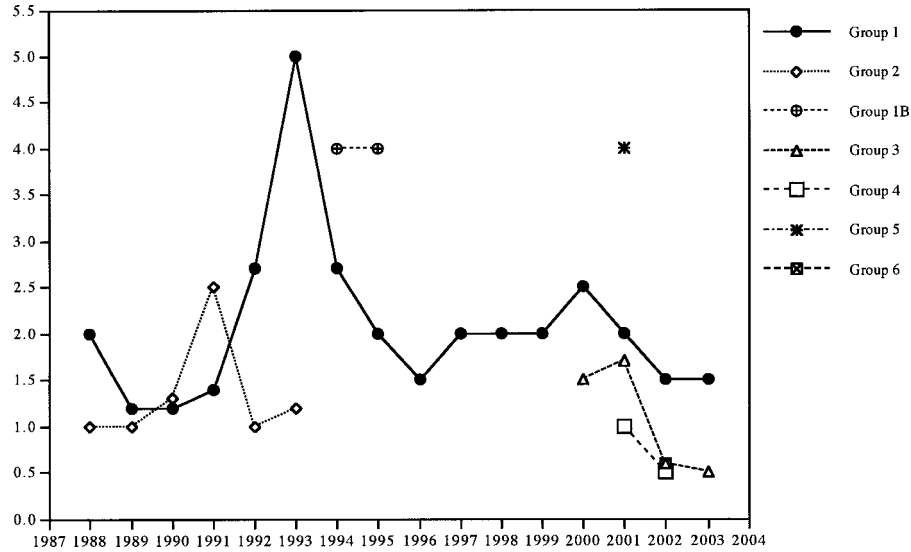


Fig. 2. Adult sex ratio in groups from July 1988 to August 2003.

TABLE 2. Birth rate^a and the adjusted birth rate^b for Group 1

Year ^c	Number of infants born	Birth rate	Adjusted birth rate
1988	2	1.00	0
1989	2	0.50	0
1990	2	0.50	1.00
1991	4	1.00	1.00
1992	1	0.25	1.00
1994	1	0.25	1.00
1996	2	1.00	0.50
1998	1	0.50	1.00
1999	1	0.50	0
2000	1	0.50	0
2001	1	1.00	1.00
2002	1	1.00	0

^a The proportion of females that gave birth in a year.

^b The proportion of infants that survived the first year of life.

^c No infants were born in 1993, 1995, and 1997.

gave birth) of Group 1 from an average rate of 0.56 during 1988 to 1993 to an average rate of 0.38 during 1994 to 2002. In addition, a growth rate for births (number of infants born/number of study years) was calculated. For 1988 to 1993 the growth rate for Group 1 was 3.17, while for 1994 to 2002 the growth rate declined to 1.44. Finally, no infants were born in Group 1 in years 1993, 1995, and 1997. These changes coincided with a drop in the average number of adult females in Group 1 from 3.1 (1988–1993) to 2.1 (1994–2002).

Disappearances, immigrations, transfers of adult individuals

Changes in the adult membership of groups occurred in both study periods (1988–1988 $n = 22$, 1994–2003 $n = 25$), but were more common between the years 1994 to 2003 (Mann-Whitney U: $Z = -1.96$, $P = 0.05$). During 1988 to 1993 we noted fifteen male and three female disappearances from study groups three immigrations of unidentified males into study groups, and the transfer of a male from one study group to another, resulting in a rate of 2.0 changes per year. Disappearances occurred at

different times throughout this time period, but immigrations and transfers happened in the months of April, May, and June, just before and during the mating period in May and June. In contrast, between 1994 and 2003 we recorded seven male and three female disappearances from study groups, ten immigrations (seven males, three females) of unidentified animals into study groups and three male and two female transfers between study groups, resulting in a rate of 8.3 changes per year. Disappearances happened throughout the year during 1994 to 2003, while transfers and immigrations all occurred between the months of October and February, which is just after the birth season in September and October. For example, in January 2002, a male from Group 4 left that group and joined a large, unknown group of uncollared individuals (two males, four females, one juvenile female, and two male infants) that we named Group 6.

Permanent group fission and new group formation

Three permanent group fissions were recorded from 1994 to 2001 (see Fig. 3). In December 1994, Group 1 fissioned along a matriline into two groups (Group 1 = four males, two females; Group 1B = four males and one female). Group 1 fissioned a second time in February 2001 along sex lines: Group 1 contained all of the group males ($n = 4$), while the females from the group ($n = 2$) were named Group 4. Group 1 temporarily migrated to outside of the Vatoharanana study area at the time that the group split, returning in December 2001 with two uncollared females. Group 4 stayed in the original home range of Group 1 and was joined by two uncollared males in April 2001. Group 3, which contained six males and three females, fissioned into two groups in October 2001. Two original female members and two original male members stayed in the group's home range and were joined by an uncollared female, while two group males joined an unknown group. We named this unknown group, which also included two uncollared males and one uncollared female, Group 5. The remaining original members of Group 3 (males = 2, females = 1) disappeared when the group fissioned.

Year	Group Fissions	Migrations In	Migrations Out	Group Disappearances
1989			Grp 1 & 2 (Apr-May)	
1990		Unknown Grp (Apr-May)		
1992			Grp 1 & 2 (Mar-Apr)	
1994				Grp 2 (Aug; 9 indiv.)
1995	Grp 1 (Dec; 11 indiv.) Grp 1 (6 indiv.) Grp 1B (5 indiv.)			Grp 1B (Mar; 5 indiv.)
2001	Grp 1 (Feb; 6 indiv.) Grp 1 (4 indiv.) Grp 4 (2 indiv.) Grp 3 (Oct; 9 indiv.) Grp 3 (4 indiv.) Grp 5 (2 indiv.)	Unknown Grp (Nov)	Grp 1 (Apr-Dec)	
2002		Unknown Grp (Jan)		Grp 4 (Jan; 4 indiv.)

Fig. 3. Permanent group fissioning, short-term group migrations in and out of the study area, and group disappearances.

Short-term group migrations and group disappearances

Groups migrated in and out of the study area on a number of occasions for periods of two to nine months at a time from 1988 to 2003 (see Fig. 3). In addition, from 1992 to 2002, three study groups disappeared from the Vatoharanana area (see Fig. 3). None of these groups, or any of their members, was seen in the study area after these dates.

Ecological factors

The proportion of trees bearing fruit for each month of the study periods was calculated to document changes in abundance from year to year and during different reproductive phases. We found there was significantly more fruit available from 1988 to 1993 (Wilcoxon's Signed Ranks Test: $Z = 3.06, P = 0.003$) compared to the 1994–2003, particularly between the months of July to November (see Fig. 4). These months correspond to the latter half of the lactation period, the period of weaning, and the first half of gestation. In addition, the proportion of trees bearing fruit was variable from year to year and inconsistent in terms of months of abundance and scarcity (e.g., years 2001–2003, Fig. 5). We also documented that *E. f. rufus* did not switch to other types of foods during periods of fruit shortage. For example, ripe and unripe fruit made up at least 79% of the diet of *E. f. rufus* during 2001 to 2003, even in year 2003 when fruit was extremely scarce (see Fig. 5). The remainder of this subspecies diet was made up of flowers, young leaves, and mature leaves.

Rainfall varied over the study years, from a low of 1,512 mm in 1988 to a high of 4,766 mm in 2002 (see Fig. 6). Cyclones and intense tropical storms occurred regularly (9 out of 16 study years), sometimes occurring in back-to-back years (e.g., 1993, 1994; 1996, 1997, 1998) and occasionally occurring more than once in a year (e.g., 1994, 2003) (see Fig. 6). However, the average amount of rainfall did not differ between noncyclone and cyclone years (noncyclone years mean = 2969.7, std dev = 950.3; cyclone years mean = 2656.8, std dev = 826.4;

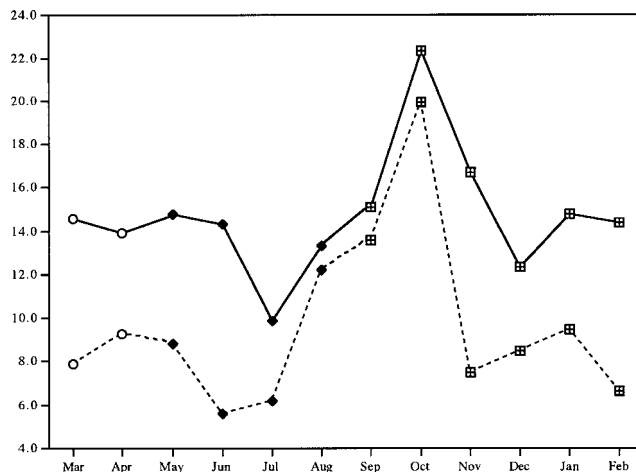


Fig. 4. The percentage of trees with fruit across reproductive and nonreproductive periods for 1988–1993 (solid line) and 1994–2003 (dashed line). Circles = nonreproductive months, diamonds = mating and gestation, squares = birth and lactation.

Wilcoxon Signed Rank Test $Z = -0.761, P = 0.45$). The number of cyclones increased over the study period from three during 1988 to 1993 (rate = 0.50) and to eight during 1994 to 2003 (rate = 0.80). Cyclones and intense tropical storms affected the Vatoharanana ecosystem, particularly in the months just after category 4 and 5 cyclones with winds that exceeded 200 km/h (Unisys Weather, 2007). The percentage of trees bearing fruit dropped immediately after large cyclones and ranged from none after cyclone Alibera (category 4) in January 1990 to only 1% after cyclone Manou (category 2) in May 2003 (see Fig. 5). Finally, although the birthrate (Table 2) was slightly lower during cyclone/tropical storm years (mean = 0.41, std dev = 0.42) compared to years without storms (mean = 0.47, std dev = 0.31), this difference was not significant (Kendall Rank Correlation: $\tau = 0.24, Z = 0.75, P = 0.45$).

Population density

The population density of *E. f. rufus* also decreased over time. Density decreased from a high of 41 individuals (per sq km) in 1991 to a low of 20 individuals (per sq km) in 1999 (see Fig. 7). In comparison, the density of *E. rubriventer* and *Varecia* increased over the study years from 15 to 25 individuals per sq km and from 2 to 10 individuals per sq km, respectively, while the density of *Propithecus* maintained at 11 individuals per sq km.

DISCUSSION

Strier (1997, 2003) has warned against compressing demographic and behavioral variables into species' averages. Further, she has pointed out that environmental stochastic changes can affect a number of variables including sex ratios within groups, dispersal patterns, breeding effort, age at maturity, survival, and population densities that may lead to "differences across populations or among studies of the same populations conducted in different years" (Strier, 2003, p 46). Certainly the behavioral flexibility we documented for the *E. f. rufus* population at Vatoharanana over a 16-year period supports her suggestion, and we propose that the key to

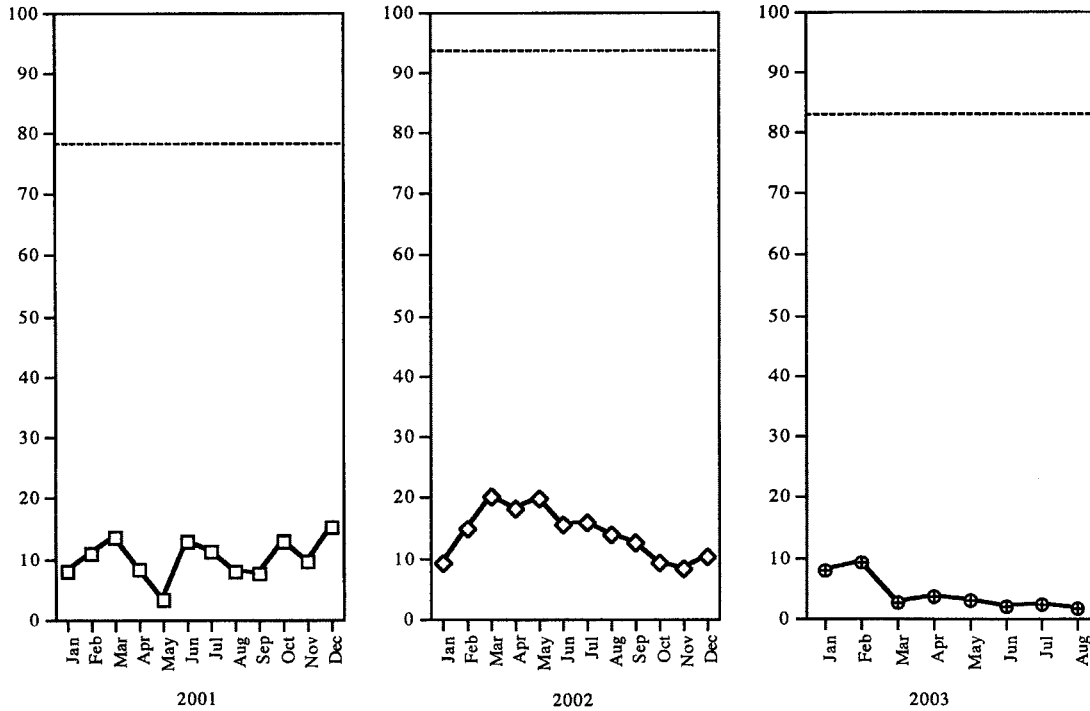


Fig. 5. The percentage of trees with fruit from January 2001 to August 2003. The dashed line across the top indicates the average amount of fruit consumption for each year. The number of trees sampled each year was 2001 = 409, 2002 = 407, and 2003 = 387.

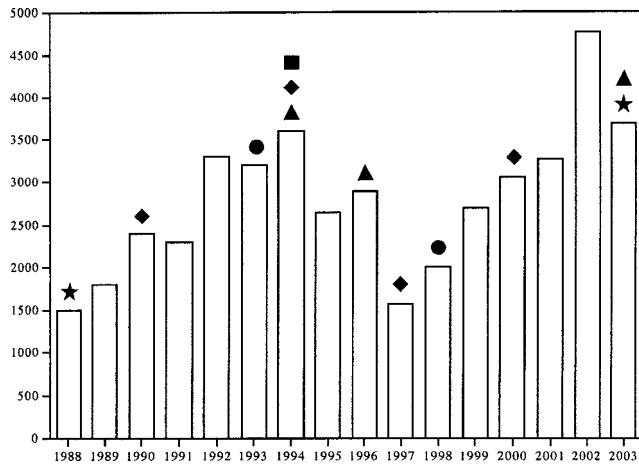


Fig. 6. Rainfall data from July 1988 to August 2003. The symbols above the bars indicate tropical storms and cyclones. Circles indicate tropical storms, stars indicate category 1 cyclones, triangles indicate category 2 cyclones, diamonds indicate category 4 cyclones, and squares indicate category 5 cyclones.

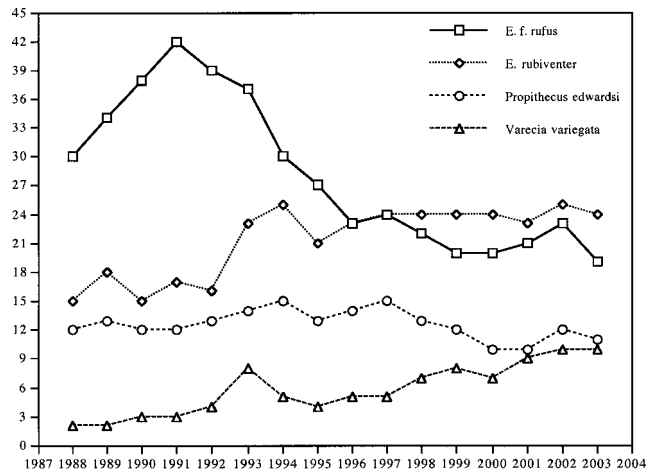


Fig. 7. Population densities (individuals per square kilometer) for frugivorous species at Vatoharanana from July 1988 to August 2003.

this flexibility seems to be the response by females to decreased fruit sources in the second half of the study.

Environmental stochasticity

The island of Madagascar has been described as a harsh and unpredictable environment (Wright, 1999) due to poor soils, low plant productivity and an erratic and severe climate (Ganzhorn et al., 1999). It is thought that these variables result in unpredictable and highly seasonal changes in food availability and low dietary di-

versity compared with other rainforests with similar sympatric primate densities (Ganzhorn, 1995a; Gould et al., 1999; Wright, 1999). In terms of fruit, density is comparatively low, there is a much longer period of time without fruits, up to 6 months a year (Wright, 1999; Wright et al., 2005), and fruit production is temporally variable from year to year (Overdorff, 1993; Ganzhorn et al., 1999; Wright, 1999) as some species produce fruit on irregular, asynchronous, or alternate year cycles (Hemingway, 1995; Overdorff, 1993, 1996; Powzyk, 1997; Balko, 1998). In the Ranomafana National Park specifically, trees fruit only about 40% of the time, with some

years of almost complete fruit failure. Low pH levels, low concentrations of potassium, and insufficient minerals may result in irregular fruiting. Although we clearly confirmed this variability in fruit production in this study, we also found that there was significantly less fruit available over time, particularly during the latter half of the lactation period, the period of weaning, and the first half of gestation. Because the energetic demands of infants increase dramatically toward the end of the lactation period (Oftedal, 1984), this probably would have been especially taxing for their mothers. Similarly, because weaning is the period when infants become juveniles, forage independently and are more vulnerable to malnutrition and infection (Janson and van Schaik, 1993), the lack of fruit sources would have made this transition difficult. Typically the weaning period for lemurs is aligned with the period of greatest resource availability (Martin, 1972; Wright, 1999; Wright et al., 2005), and small-sized fruits usually peak in abundance at the beginning of the weaning period (Wright, 1999; Wright et al., 2005).

The seasonality and variation in fruit production is tied in part to climatic variables such as cyclone-related plant damage. Cyclones and tropical storms are yearly experiences in Madagascar, typically occurring between the months of January to March (Donque, 1972; Jury, 2003). Direct hits from cyclones can cause complete defoliation, tree falls, postcyclone tree mortality and total tree loss (Ganzhorn, 1995b). This can mean that neither fruits nor leaves may be available for consumption by lemurs, with only crisis foods, such as epiphytes, available until the next spring (Ratsimbazafy, 2002). In this study, there was an increase in the number of cyclones from 1994 to 2003 and we found a significant difference in fruit availability during these years compared to 1988 to 1993. The decrease in fruit availability is correlated with a 46% decline in average group size. Similarly at the Manombo Reserve, Ratsimbazafy (2002) found that shortly after cyclone Gretelle in 1997, which destroyed 80% of the emergent and canopy layers, there was a marked decrease in fruit production and populations of day active lemurs fell by more than half. Hurricane Iris had an even more severe affect on the *Alouatta pigra* population of Monkey River in southern Belize, as the fruit supply was devastated (Pavelka and Behie, 2005) and 88% of the population lost (Pavelka et al., 2007). Such natural disasters can have important impacts on the sizes and densities of populations and groups and on the age and sex ratios within groups (Wright, 1999).

Responses to resource changes

Lemurs have evolved ways to cope with seasonal climatic and resource changes. To survive lean months when little to no available fruit is available, many lemurs may switch to low quality foods such as leaves (Richard, 1978; Meyers and Wright, 1993; Hemingway, 1996; Atsalis, 1999; Gould et al., 1999), shift their diet components (Overdorff, 1993; Tan, 1999), use food patches of different sizes, fission into subgroups when feeding (Moreland, 1991; Vasey, 1997, 2003; Balko, 1998) reduce their activity and metabolism (Pereira et al., 1999; Schmid, 2000; Dausmann et al., 2005), and/or increase or decrease day ranges (Corbin and Schmid, 1995). What appears to be uncommon for primate groups, however, is "habitat shifting" or traveling outside of their home ranges, or moving between habitats,

in search of resources (Hemingway and Bynum, 2005). Habitat shifting is limited to relatively aseasonal environments and habitat shifters, typically live in polygynous, multimale-multifemale groups, have broadly defined home ranges, and exhibit spatial and temporal patterns of home range use in response to food scarcity. Habitat shifting is primarily concentrated in the New World primates (*Callicebus torquatus* Kinzey, 1977; *Cebuella pygmaea* Soini, 1993; *Saimiri* sp., *Cebus albifrons*, *Cebus apella* and *Lagothrix lagotricha* Peres, 1994; *Alouatta seniculus* Palacios and Rodriguez, 2001), probably because the short time between peak leaf flush and peak fruiting restricts their ability to increase their dietary diversity (van Schaik and Pfannes, 2005).

Habitat shifting seems to be the main response of *E. f. rufus* to dietary stress (Overdorff, 1993; Overdorff et al., 1999; this study). Several of our study groups increased their ranges and eventually migrated up to 5 km away from their home ranges when there were two or fewer species of fruit in season, presumably to areas with more abundant fruit sources (Overdorff, 1993; this study). Hemingway and Bynum (2005) point out that habitat shifting allows *E. f. rufus* groups to stay together as they travel increasingly further distances in search of fruit sources, and suggest that this subspecies follows an energy maximizing strategy since they increase their ranging to meet their nutritional needs. As female *E. f. rufus* are primarily responsible for leading group movements to food sources (Erhart and Overdorff, 1999; Scholz and Kappeler, 2004), they may be able to influence their daily foraging efficiency and nutritional intake, which could influence long-term reproductive success (Erhart and Overdorff, 1999). We suggest that female nutritional needs may determine ranging behavior to a large extent in eastern *E. f. rufus*, at least during months of gestation and lactation. At present, habitat shifting has not been documented for western, dry forest *E. f. rufus* (Sussman, 1974; Gerson, 2000), even though average group size between eastern and western populations is relatively the same (Sussman, 1991; Overdorff, 1993). Resource availability seems to fluctuate more in the eastern evergreen forests compared with the western deciduous forests (Jolly et al., 1982; Richard et al., 1991; Sussman, 1991), and is seasonally unpredictable (Jolly, 1984; Hemingway and Overdorff, 1999; Wright, 1999). Further, this difference may be related to dietary differences as western populations consume a higher yearly percentage of leaves compared with eastern populations. The protein to fiber ratio in leaves from the western deciduous forests are greater than the eastern evergreen forests, and thus provides a better nutritional base for parts of the year (Ganzhorn, 1992; Ganzhorn et al., 2003) and may obviate the need for habitat shifting.

An alternative tactic to dealing with reduced food resources would be to decrease group size (Kappeler and Heymann, 1996). If group size is adjusted to the available food supply, then greater resource competition should result in higher emigration rates and decreased birth rates as preferred foods become scarcer. Certainly, disappearance, transfer and immigration are consistent features of *E. f. rufus* male life history (Overdorff et al., 1999; Ostner and Kappeler, 2004). We found that the frequency of these changes became even more common for males over the study period, perhaps as males searched for groups with a greater number of resident females. In contrast, while there were no instances of female immi-

gration into, or transfer between, study groups from 1988 to 1993, *E. f. rufus* females left groups and changed groups as fruit became scarcer over time. Because this species does not have counterstrategies to food competition such as female dominance or female bonding, then a group may only be able to support two or three adult females (Overdorff et al., 1999). Thus, during the latter half of the study there were fewer females in study groups, fewer females reproduced each year and females only reproduced in consecutive years when they lost an infant in the first year of life. As a result, the interbirth interval increased over time. The decline in the birth and growth rates that we documented are sensible as successful reproduction depends upon the storage of resources and amount of energy expenditure during prenatal (Young et al., 1990) and postnatal stages (Kappeler, 1996). From 1994 to 2003, six of the seven reproductive aged females weighed less than 2.3 kg, the minimum body weight that Overdorff et al. (1999) suggested is necessary for successful reproduction on a yearly basis. Similar reductions in reproduction related to severe seasonal food shortages have been reported for *Lemur catta* (Gould et al., 1999; Jolly et al., 2002), *Propithecus verreauxi* (Richard et al., 2002), and *Varecia variegata* (Ratsimbazafy, 2002). Finally, permanent group fissioning in *E. f. rufus* seems to be linked to the number of males in groups as fissioning occurred when groups contained two times more males than females. Although additional males may benefit females in several ways such as 1) support when intergroup food competition is high (Overdorff et al., 1999), 2) reduction of intragroup feeding interference (Pereira and McGlynn, 1997; Overdorff, 1998), and 3) protection of females and their infants from infanticidal, immigrant males (Ostner and Kappeler, 2004), there may be a limit to the number of males a group can contain.

Population density changes

The population density of *E. f. rufus* decreased by 50% over the study period, while the density of *E. rubriventer* and *Varecia variegata* increased over time. Why these differences exist is not clear, but they may be linked to anthropogenic disturbance, predation pressure, and ecological changes. Historically, anthropogenic disturbance of the Ranomafana forest and the lemurs within it occurred through use of forest products, selective logging and hunting (Wright, 1992). However, such activities have decreased since this area became a national park in 1991, and we do not think that they have had much of an impact on the existing *E. f. rufus* population at Vatoharanana. Nor do we think that predation is the root cause of the changes in lemur densities at the study site for several reasons. Although there is one mammalian carnivore (*Cryptoprocta ferox*) and two raptors (*Polyboroides radiata*, *Accipiter henstii*) that are known to predate on large-bodied lemurs (Karpanty and Wright, 2007), none are abundant at the study site (Wright, 1998), the predation rate for *E. f. rufus* by raptors is not significantly different from those of *E. rubriventer*, *P. edwardsi*, and *V. variegata* (Karpanty, 2006), and there have been no documented kills of *E. f. rufus* by *Cryptoprocta* (Wright, 1998). Rather, the majority of documented *Cryptoprocta* kills have been on *P. edwardsi*, which has the largest mass (5,800 g) and biomass (125.0 kg/km²) of the lemurs in the Ranomafana National Park (*E. f. rufus* mass = 2,200 g, biomass = 66.0 kg/km²).

Therefore, we suspect that ecological changes, particularly in fruit abundance, have had a greater influence on lemur population densities at Vatoharanana. It is the case that *E. f. rufus* groups are larger than those of *E. rubriventer*, and Overdorff (1993) has suggested that easily digested foods may be depleted before all *E. f. rufus* group members have been satiated, while the opposite may be the case for *E. rubriventer*. Thus, the scarcity of fruit over the study period may have resulted in smaller *E. f. rufus* groups and a lower population density. *V. variegata* numbers may have increased as the forest of Vatoharanana began to recover from selective logging that occurred from 1987 to 1988. Logging had resulted in a decreased availability of preferred *V. variegata* food tree species in the Vatoharanana area (White et al., 1995; Balko, 1998). In addition, it has been our experience that *E. f. rufus* groups never win contests over fruit sources with *V. variegata*, even when confronting a subgroup of *Varecia* (Overdorff and Erhart, unpubl. data). But regardless of the explanations as to why *E. f. rufus* density decreased over the study period, it is important to remember that few primate populations are numerically stable over time (Altmann and Altmann, 1979; Dunbar, 1988; Strier, 2003; Jones, 2005). Therefore, we would expect the *E. f. rufus* population size to oscillate over time, growing and shrinking in response to stochastic variables.

CONCLUSIONS

Behavioral flexibility may be favored when abiotic (e.g., weather) and biotic (e.g., plant phenology) variables fluctuate over very short periods of time (Jones, 2005). We suggest that female behavioral responses to changes in fruit availability may in part drive some of the demographic changes we documented in this study. However, we must acknowledge the limitations of our dataset. Although the time span of this study was 16 years, the average life span for *E. f. rufus* is 30.8 years (Harvey et al., 1987); therefore, a longer length of time is necessary to more fully understand the behavior and demography of this subspecies. In addition, we were only able to observe a total of 54 individuals over the course of our study. As pointed out by Pochron et al. (2004), sample size quickly diminishes as data are broken down into age and sex classes, which negatively impacts data quality. Lifetime knowledge of individuals is also critical to our understanding of demography, as is the integration of behavior, ecology and demographic information (Altmann and Altmann, 1979; Dunbar, 1979; Lee and Kappeler, 2003; Strier, 2003; Jones, 2005; Strier et al., 2006). Thus, future analyses we intend to augment the existing data set on *E. f. rufus* at Vatoharanana and examine the potential costs and benefits to individual males and females in larger and smaller groups in terms of foraging efficiency and lifetime reproductive success. In the meantime we hope that the results of this study, particularly the 50% drop in population density, will be incorporated in the conservation management of *E. f. rufus*.

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