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## Distribution of Ruffed Lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar

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### Key Words

Selective logging • Habitat disruption • Frugivory • *Varecia* • Ruffed lemurs • Madagascar

### Abstract

The distribution of *Varecia variegata* at 3 sites in Ranomafana National Park is consistent with the hypothesis that this specialized frugivore is the most susceptible of 12 sympatric lemur species to habitat disruption brought about by selective logging. *Varecia* is most abundant at the least disturbed site and absent from the most intensively logged site. The logged area showed lower values for overall tree basal area, crown diameters and tree height and an increase in the number of trees, presumably because of growing saplings. *Varecia* select large food trees of species that are preferentially logged. Although tree species diversity may be higher after logging, many *Varecia* food trees were absent from disturbed forests.

### Introduction

*Varecia variegata variegata* has been reported in the eastern rain forest of Madagascar from the Antainambalana River in the north to Manakana [1] and to the Mananara River in the south [2–4]. Densities and distributions of *Varecia* within this range are unknown but are thought to be generally low and discontinuous [3, 5–7]. The introduced population on the island of Nosy Mangabe, however, shows high densities of as many as 20–30 individuals per square kilometer [6–9].

The current distribution of prosimian primates in Madagascar is highly affected by habitat destruction [6]. The specific impact of selective logging on prosimian primates has not been studied, although information is available for nonprosimian primate populations in many forested areas [for review, see 10]. Large-bodied frugivores are most susceptible to disturbance from logging in many rain forests. *V. variegata variegata* is the most frugivorous large-bodied representative among the 12 species of prosimians in Ranomafana National Park [11, 12]. In this paper, information is presented on the distribution and densities of *V. variegata variegata* at 3 sites within one contin-

uous block of eastern rain forest. This distribution is compared to forest differences among forest types produced by selective logging at one of the sites within the park.

## Methods

The Ranomafana National Park is a 40,000-ha section of rain forest located between 47° 18' to 47° 37' East and 21° 2' to 21° 25' South. The park is a continuous tract ranging from montane rain forest at 1500 m to lowland rain forest at 500 m elevation. The 3 sites examined were Talatakely (TALA), Vatoharanana (VATO) and Valohoaka (VALO) located at increasing distances from a main road that bisects the park (approx. 1, 5 and 11 km, respectively). *Varecia* were present at VATO and VALO but not at TALA. The degree of habitat disturbance was assessed based on park records, local knowledge of logging activity and the density of cut trees and log-processing sites. The TALA site has two levels of disturbance: selectively logged (TALA1) and intensively logged (TALA2). The VATO site has less habitat disruption and was the first location where *Varecia* were observed. The VALO site had the least habitat disruption.

Forest composition and structure were assessed in two 25×25 m and eight 50×5 m quadrats at VATO and at two 25×25 m quadrats at TALA (TALA1 in a less intensively logged area and TALA2 in a more intensively logged area). The 25×25 m quadrats were part of a study of *Varecia* (by F.J.W.), whereas the 50×5 m quadrats were established for a long-term study of the phenology of the VATO site (by D.J.O.). Comparable measures were taken at both sites, and methodology was standardized by two of the authors (D.J.O. and F.J.W.) jointly measuring and estimating the trees in one 25×25 m VATO quadrat. Every tree above 2.5 cm diameter at breast height (DBH) was selected. The DBH was measured and the Malagasy species name recorded. Crown shape, radius and depth in meters were estimated visually. The degree of continuity in the canopy layer within each quadrat was estimated by recording whether or not any given tree canopy was in contact with an adjacent tree canopy. Flowers, fruits and leaves of many plant species were collected where possible and sent to the Missouri Botanical Garden and Park Tzimbazaza for identification. Malagasy vernacular names are given for species that have yet to be identified.

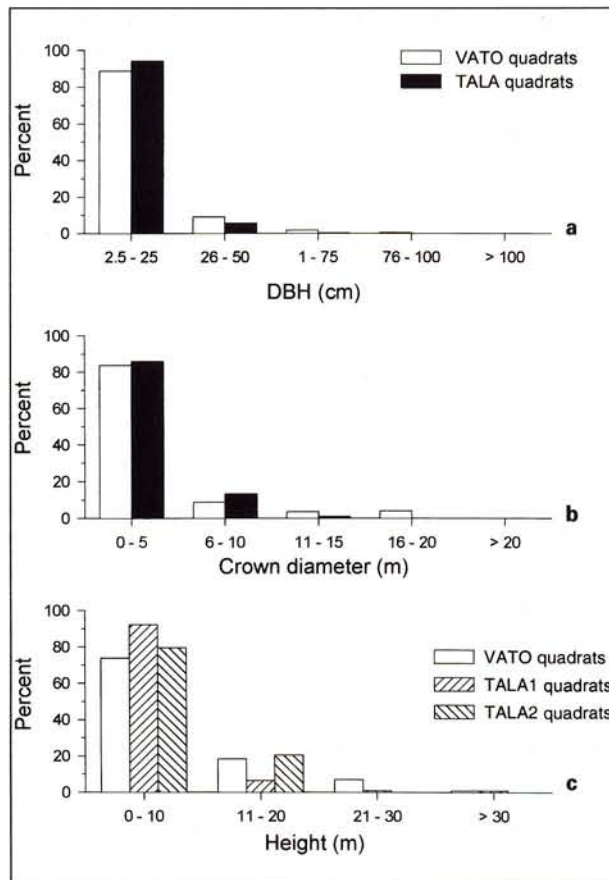
All quadrats were established in 1988. *Varecia* were observed at VATO for 112 h from June to August 1988 and at VALO for 605 h from September to November 1990. All trees fed in by *Varecia* at both VATO and VALO were identified, the DBH measured, and height, radius and canopy volume visually estimated.

Frequency distributions of tree sizes were compared using the test of independence for differences among sites, while goodness-of-fit G tests were used to assess the fit between the frequency distributions of *Varecia* food trees at VATO and the quadrat distributions at VATO. All tests were performed with the Williams correction. Where appropriate for tests of independence, unplanned tests of all subsets of rows and columns in the observed data by the simultaneous test procedure were performed to identify subsets of the data that were not significantly dependent [13]. Mean values are given for tree measures.

## Results

The frequency distributions of the two TALA quadrats did not differ for DBH and crown diameter ( $G = 2.142$ ,  $0.5 < p < 0.1$ , not significant, and  $G = 0.564$ ,  $0.9 < p < 0.5$ , not significant, respectively). These data were, therefore, pooled for comparisons with the VATO quadrats. The data for tree height were not pooled as the frequency distributions differed between the two TALA sites ( $G = 11.410$ ,  $p < 0.005$ ). Although the mean heights for the two TALA sites were similar (see below), TALA1 contained more short trees and fewer taller trees than TALA2.

The VATO and TALA sites differed significantly for DBH ( $G = 10.168$ ,  $p < 0.01$ , fig. 1a), with the VATO site containing more large trees than TALA (VATO mean



**Fig. 1.** Frequency distributions of trees in quadrats at VATO and TALA. **a** DBH. **b** Crown diameter. **c** Tree height.

DBH 123.3 cm and TALA mean DBH=21.5 cm). The two areas also differed in crown diameter ( $G = 27.704$ ,  $p < 0.001$ , fig. 1b), with the VATO site containing more large trees (VATO mean diameter 1.8 m and TALA mean diameter 1.7 m). VATO, TALA1 and TALA2 heights were significantly different ( $G = 50.387$ ,  $p < 0.001$ , fig. 1c), with the VATO site having more tall trees than either TALA site (VATO mean height 9.1 m, TALA1 mean height 6.7 m and TALA2 mean height 7.0 m). There were no nonsignificant subsets containing all height classes so that no two sites had similar frequencies of tree heights.

There were 2,163 trees/ha in the VATO quadrats, 2,256/ha in TALA1 and 2,896/ha in TALA2. The total basal area at each site was  $60 \text{ cm}^2/\text{m}^2$  at VATO,  $36 \text{ cm}^2/\text{m}^2$  in TALA1 and  $35 \text{ cm}^2/\text{m}^2$  in TALA2.

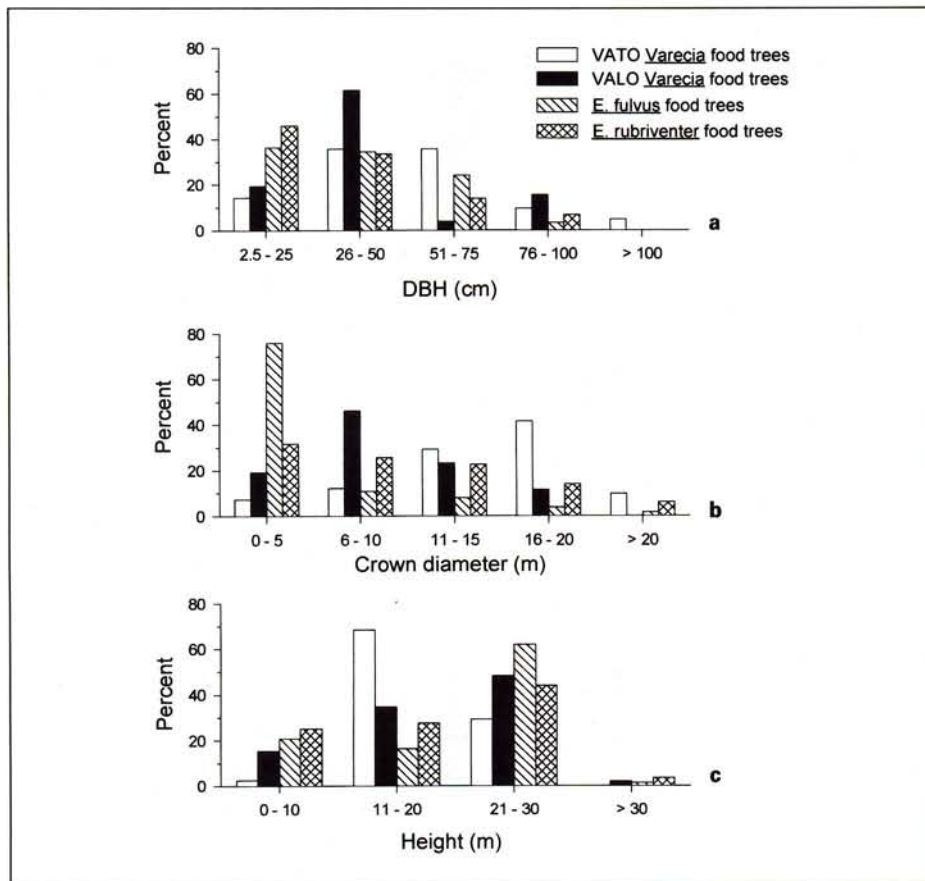
There were 86 plant species in the VATO quadrat and 43 species in the two TALA quadrats. This represents 264.6 species/ha at VATO and 344.0 species/ha at TALA. 41.6% of *Varecia* food tree species were present at both VATO and TALA, but 36.1%

**Table 1.** List of plant food species eaten by *Varecia*

Vernacular	Family	Genus and	species	Food type	VATO	VALO
Ambilazona	Fabaceae	<i>Calliandra</i>	<i>alternans</i>	flowers		+
Dendemilahy	Loganiaceae			fruits	+	
Fanalamangidy	Canellaceae			fruits		+
Fatora	Rubiaceae	<i>Mussaendra</i>	sp.	fruits	+	+
Fatsikahitra g.f.	Rubiaceae	<i>Canthium</i>	<i>baxifolium</i>	fruits		+
Hafotra makoroho	Sterculiaceae			fruits		+
Hafotra makoroho	Sterculiaceae			flowers		+
Hazomena	Meliaceae	<i>Khaya</i>	<i>madagascarensis</i>	fruits		+
Kalafana	Myrsinaceae	<i>Oncostemon</i>		fruits		+
Kalamasimbarika	Melastomaceae	<i>Medinilla</i>	sp.	fruits		+
Kimba	Clusiaceae	<i>Symphonia</i>	sp.	leaves	+	+
Masiposaima				leaves	+	
Nato	Sapotaceae	<i>Sideroxylon</i>	sp. 1	nectar	+	+
Nato	Sapotaceae	<i>Sideroxylon</i>	sp. 2	nectar	+	+
Nato	Sapotaceae	<i>Sideroxylon</i>	sp. 1	fruits		+
Nonoka	Moraceae	<i>Ficus</i>	<i>pyrifolia</i>	fruits	+	+
Rahiaka	Sapotaceae	<i>Gambeya</i>	<i>madagascarensis</i>	fruits	+	
Ramidriona	Proteaceae	<i>Dilobeia</i>	<i>thouarsii</i>	leaves	+	
Ramy	Burseraceae	<i>Canarium</i>	<i>madagascarensis</i>	fruits	+	+
Ramiavotoholo				leaves		+
Ramiavotoholo				fruits		+
Rotra fotsy	Myrtaceae			fruits	+	+
Sehana	Anacardiaceae			fruits		+
Shandramy	Leguminaceae	<i>Albizia</i>	sp.	fruits		+
Sandramy	Anacardiaceae			fruits	+	
Tambarasy				fruits		+
Tavolomaintra	Lauraceae	<i>Ravensara</i>	sp.	leaves	+	+
Tavolomavravena	Lauraceae			fruits		+
Tavolomavravena	Lauraceae			leaves		+
Tavolopina	Lauraceae	<i>Ocotea</i>	sp.	leaves	+	
Tavolorani	Lauraceae			fruits		+
Tavolorano	Lauraceae	<i>Ravensara</i>	sp.	fruits	+	+
Tongolahy	Loranthaceae	<i>Bakerella</i>	sp.	fruits		+
Vahibanicumba				fruits		+
Vahimberana	Papilionaceae	<i>Stongylodon</i>	sp.	flowers		+
Vahimberana	Papilionaceae	<i>Stongylodon</i>	sp.	nectar		+
Vahimvolaka				fruits		+
Vahivoraka	Acanthaceae	<i>Mendonsia</i>	<i>couvani</i>	fruits		+
Varongy	Lauraceae	<i>Ocotea</i>	sp.	fruits	+	
Voara	Moraceae	<i>Ficus</i>	sp.	fruits	+	+

of *Varecia* food tree species were present only at VATO. These food species that were not present at TALA accounted for 27% of focal animal feeding and 2 of the 5 most preferred food species at the VATO site.

Most trees in the VATO quadrats were in contact with a neighboring tree (97.7%,  $n = 827$ ). In TALA1, 72.3% ( $n = 137$ ) of trees contacted another tree, whereas in TALA2 only 67.9% of trees were in contact ( $n = 165$ ).

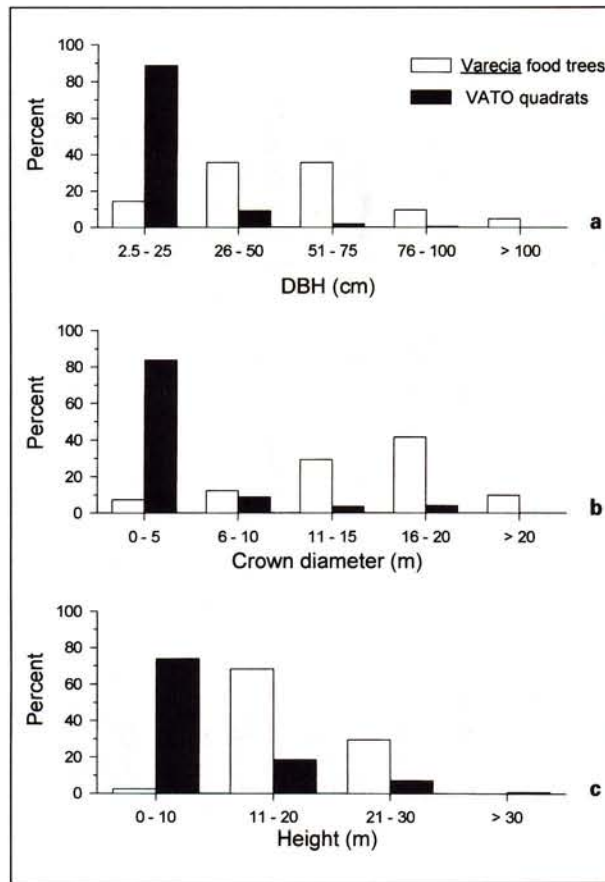


**Fig. 2.** Frequency distributions of food trees for *Varecia* at VATO and VALO and for *E. fulvus* and *E. rubriventer* at VATO. **a** DBH. **b** Crown diameter. **c** Tree height.

The density of *Varecia* was 1.0 individual/km<sup>2</sup> at VATO and 16.2 individuals/km<sup>2</sup> at VALO. Between VALO and VATO, *Varecia* fed on 36 different plant species. 25% of species were eaten at both sites (table 1). These species accounted for 63% of focal animal feeding at the VATO site and included the 2 most preferred food species. Taking both sites together, *Varecia* ate fruit from 69.4% of plant species.

The two sites differed in the size of fruit trees used by *Varecia*. *Varecia* fed in shorter trees ( $G = 11.916$ ,  $p < 0.01$ ) with smaller DBH ( $G = 17.182$ ,  $p < 0.001$ ) and crown diameter ( $G = 24.299$ ,  $p < 0.001$ ) at VALO than at VATO (fig. 2a–c).

The frequency distributions of *Varecia* food trees at the VATO and VALO sites were significant different from those at the VATO quadrats for DBH ( $G = 136.764$ ,  $p < 0.001$ , fig. 3a), crown diameter ( $G = 142.638$ ,  $p < 0.001$ , fig. 3b) and height ( $G = 97.182$ ,  $p < 0.001$ , fig. 3c).



**Fig. 3.** Frequency distributions of *Varecia* food trees at VATO and of trees in VATO quadrats. **a** DBH. **b** Crown diameter. **c** Tree height.

## Discussion

The differences between disturbed (TALA) and less disturbed (VATO) quadrats suggest that logging reduces average tree size and height. The most intensively logged site (TALA2) had lower tree heights but no difference in DBH or crown diameter compared to the less intensively logged site (TALA1).

Although the average height of trees was modified by logging, the density of trees did not appear to be markedly affected. This presumably reflects the regrowth of numerous saplings in the logged areas as compared with the less logged areas. This interpretation is supported by figures for the total basal area at each site, which decreased as the degree of logging increased.

Logging also disrupted the canopy. This change was noticeable not only in the comparison between VATO and TALA but also between the two sites at TALA, with the most logged site having 32.1% of trees without a continuous canopy. This disruption of the canopy may seriously affect an arboreal quadruped such as *Varecia* [14].

However, other prosimians are able to adapt to the difference in forest structure between TALA and VATO. For example, *Eulemur fulvus* and *E. rubriventer* leap more, use more vertical clinging postures and are less quadrupedal at the more logged TALA site than at the less logged VATO [15]. *Varecia* may be absent from the more logged site because it was unable to adapt to a habitat more suitable for vertical clinging postures.

It is difficult to compare the species diversity of quadrats between sites because of the differing sizes of quadrats used. Species diversity does not, however, appear to be lower at the logged site. Despite the higher species density at TALA, fewer *Varecia* food trees were found in the quadrats at TALA than at VATO. This may be a reflection of the smaller total quadrat size used there, but it may also indicate that a significant component of the plant species diversity at TALA is due to postlogging colonization by tree species not found in less logged forests.

*Varecia* fed in the larger, taller trees at VATO compared to the general profile for trees measured in the VATO quadrats. Comparing VALO and VATO, *Varecia* were found to be more abundant at the less disturbed site (VALO) but fed in somewhat larger trees at the more logged site (VATO). This may reflect differences in fruit availability in this highly seasonal forest, as the two studies were conducted at different times in different years.

Two other sympatric diurnal frugivores, *E. fulvus* and *E. rubriventer*, use species of fruit trees similar to those used by *Varecia* [16]. At VATO, however, both *Eulemur* species fed in trees with a smaller average DBH ( $G = 52.094$ ,  $p < 0.001$ ) and crown diameter ( $G = 87.098$ ,  $p < 0.001$ ; fig. 2) than those in which the sympatric *Varecia* fed. These trees were not shorter as both *Eulemur* species fed in more trees in the 21- to 30-m height class than did the *Varecia* (fig. 2). This specialization by *Varecia* on larger, but not taller, food trees does not, therefore, simply reflect a frugivorous diet. Feeding in the large trees that occur at low density in the forest at VATO is associated with the large home ranges (197 ha) of *Varecia* at VATO [12].

The results of these comparisons were consistent with the hypothesis that *Varecia* does not occur at the TALA site because logging has reduced the availability of preferred food trees. The habitat degradation may also disrupt travel routes of *Varecia* through the canopy.

There are many alternative hypotheses to explain the differential distribution of *Varecia* within the Ranomafana National Park. There may be substantial natural habitat differences between sites, or differential past hunting pressure could possibly explain this patchy distribution. However, none of the other 11 prosimian species shows this break in distribution between TALA and VATO, although there may be differences in their abundance between the sites. This suggests that there are differences between the sites that only have an effect on the specialized frugivore of the prosimian community.

Habitat disruption has also brought introduced species such as Chinese guava (*Psidium cattleianum*) into TALA but not VATO. This species produces a large fruit crop that is used by many of the prosimian species. Although this introduced species may exert some influence on the ranging and feeding of the prosimians that are present at TALA, it does not seem likely that its presence has led to the exclusion of *Varecia* from the site.

Selective logging targets large trees and particular species. *Varecia* appears to be differentially affected because of the loss of these large trees but may also be affected by the logging of selected precious hardwoods that are important food trees. For ex-

ample, nato (*Sideroxylon*) and ramy (*Canarium madagascarensis*) are important *Varecia* food trees that are targeted for selective logging, especially for use in construction. Like other large frugivores, therefore, *Varecia* appears to be particularly susceptible to logging [10]. It may therefore be possible to use *Varecia* as an indicator species to assess the degree of habitat disruption.

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## References

- 1 Petter A, Petter JJ: Infraorder Lemuriformes; in Meester J, Setzer HW (eds): The Mammals of Africa: An Identification Manual. Washington, Smithsonian Institution Press, 1971, pp 1–10.
- 2 Petter JJ, Albignac R, Rumpel Y: Faune de Madagascar. Paris, CNRS, Orstom, 1977, vol 44: Mammifères Lémurien.
- 3 Tattersall I: The Primates of Madagascar. New York, Columbia University Press, 1982.
- 4 Petter JJ, Petter-Rouseaux A: Classification of the Prosimians; in Doyle GA, Martin RD (eds): The Study of Prosimian Behavior. London, Academic Press, 1979, pp 1–44.
- 5 Tattersall I: Distribution of the Malagasy lemurs. 1. The lemurs of northern Madagascar. Ann NY Acad Sci 1977;293:160–169.
- 6 Harcourt C, Thornback J: Lemurs of Madagascar and the Comoros. The IUCN Red Data Book. Gland, IUCN, 1990.
- 7 Simons HJ, Lindsay NBD: Survey work on ruffed lemurs (*Varecia variegata*) and other primates in the northeastern rain forests of Madagascar. Primate Conserv 1987;8:88–91.
- 8 Morland HS: Parental behavior and infant development in ruffed lemurs (*Varecia variegata*) in a northeast Madagascar rain forest. Am J Primatol 1990;20:253–265.
- 9 Morland HS: Preliminary report on the social organization of ruffed lemurs (*Varecia variegata variegata*) in a northeast Madagascar rain forest. Folia Primatol 1991;56:157–161.
- 10 Johns AD, Skorupa JP: Responses of rain-forest primates to habitat disturbance: A review. Int J Primatol 1988;8:157–191.
- 11 Glander KE, Wright PC, Daniels PS, Merenlender AM: Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. J Hum Evol 1992;22:1–17.
- 12 White FJ: Social organization, feeding ecology and reproductive strategy of ruffed lemurs, *Varecia variegata*; in Ehara A, Kimura T, Takenaka O, Iwamoto M (eds): Primatology Today: Proceedings of the XIIIth Congress of the International Primatological Society, Nagoya and Kyoto, 18–24 July 1990. Amsterdam, Elsevier Science Publishers, 1991, pp 81–84.
- 13 Sokal RR, Rohlf FJ: Biometry, ed 2. New York, Freeman and Co, 1981.
- 14 Dagosto M: Locomotion of *Propithecus diadema* and *Varecia variegata* at Ranomafana National Park, Madagascar. Am J Phys Anthropol 1989;78:209.
- 15 Dagosto M: Testing positional behavior of Malagasy lemurs: A randomization approach. Am J Phys Anthropol 1994;94:189–202.
- 16 Overdorff DJ: Ecological Correlates to Social Structure in Two Prosimian Primates in Madagascar: *Eulemur fulvus rufus* and *Eulemur rubriventer*; PhD thesis Duke University, 1991.

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