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Habitat Utilization of Blue-eyed Black Lemurs, *Eulemur macaco flavifrons* (Gray, 1867), in Primary and Altered Forest Fragments

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Abstract: Lemurs of the genus *Eulemur*, including *Eulemur macaco*, are usually considered to be generalized, opportunistic frugivore-folivores, with a high degree of ecological flexibility. They are thus regarded as being able to adapt to a range of habitat types, and therefore less affected by the loss of primary forest habitat. In this study we assessed the suitability of altered forest habitat for the blue-eyed black lemur (*Eulemur macaco flavifrons*) on the Sahamalaza Peninsula (northwest Madagascar). Our aims were to identify structural vegetation characteristics that are important for the taxon, and to compare their availability in a primary and a secondary forest fragment. Home range size and habitat use of four groups of *E. flavifrons*, the availability of food resources and sleeping trees, as well as plant biodiversity and plant communities were investigated. The forest fragments harboring *E. flavifrons* groups differed in a number of structural variables. The density of food and resting trees was higher in primary forest. Home range size of blue-eyed black lemurs was larger in secondary forest. The lemurs used both habitat types differently. In the primary forest fragment the number of plant families and trees used for feeding or resting was higher. The results indicate that although *E. flavifrons* seems to be an edge-tolerant subspecies, the taxon nevertheless shows some degree of habitat specialization. The lower density of blue-eyed black lemurs in the secondary forest fragment indicates that this type of habitat is only of limited value to *E. flavifrons*.

Key words: Madagascar, *Eulemur macaco flavifrons*, primary forest, secondary forest, habitat generalist, habitat specialist

Introduction

The genus *Eulemur* is medium-sized, with a weight of 1.0–2.5 kg, and occurs in almost all forested areas of Madagascar (Glander *et al.* 1992; Terranova and Coffman 1997). These lemurs are often considered to be generalist, opportunistic frugivore-folivores (for example, Overdorff [1988] for *E. rubriventer*; Vasey [1997] for *E. albifrons*; Mittermeier *et al.* 2006). It is commonly suggested that these species show a high degree of ecological flexibility and can adapt well to different habitat types, including secondary forest and plantations (for example, Sussman and Tattersall [1976] for *E. mongoz*; Mittermeier *et al.* 2006). Some species, such as *E. sanfordi*, even appear to favor secondary forests (Freed 1996). Such behavioral and ecological flexibility is also reported for some other lemur genera, for example by Irwin and Raharison (2006) for *Propithecus diadema*, and by Feistner and Mutschler (2000) for *Hapalemur occidentalis*. Despite these findings, however, there are still very few data on how different lemur species respond to habitat degradation and on whether different species can use regenerating or replanted forests (Ganzhorn 1987; Ganzhorn and Abraham 1991; Ganzhorn *et al.* 1997; Andrianasolo *et al.* 2006). This is because the resources which represent essential or limiting factors for different lemurs are poorly understood (Andrianasolo *et al.* 2006). Knowledge of these issues can have significant implications for conservation and natural resource management decisions. If a primate species shows a high degree of ecological flexibility, it will probably be less affected by the loss of its original habitat than one that relies on certain structural vegetation characteristics present only in certain forest types. Rendigs *et al.* (2003) emphasized the importance of microhabitat analyses for lemur conservation. Secondary forest is often of limited value to mouse lemurs (*Microcebus maurus*) as buffer zones or even corridors (Ganzhorn and Schmid 1998). According to Andrianasolo *et al.* (2006), more specialized lemurs may require specific habitat structures. Such habitat
specialists select patches of usable habitat and there are higher population densities if suitable microhabitats are available. Habitat generalists, on the other hand, are not expected to differ in population density as a consequence of habitat structure and should not co-vary with the structure of different forest types.

The size of home ranges in the frugivorous and foliovorous Lemuridae is generally highly variable and appears to depend on habitat type (Curtis and Zaramody 1998). Home ranges seem to be large in eastern rain forest habitats and in the southern xerophytic zone of Madagascar, whereas they appear to be smaller in the seasonal forests of western Madagascar (although group sizes of Eulemur taxa are similar in both habitats). According to Curtis and Zaramody (1998), this could imply a more abundant and perhaps uniform distribution of the main food resources in seasonal western forests throughout the year.

Home range size is frequently cited as influencing a species’ ability to live and survive in a fragment (Lovejoy et al. 1986; Estrada and Coates-Estrada 1996; Chapman et al. 2003). Primate groups and densities appear to be smaller in secondary than in primary forests (for example, Estrada and Coates-Estrada 1995; McCann et al. 2003; Rodríguez-Toledo et al. 2003), which in turn suggests that a larger home range is necessary to sustain the same number of individuals in a secondary forest.

Blue-eyed black lemurs, Eulemur macaco flavifrons (Gray 1867), are found only in the semi-deciduous forests on, and just east of, the Sahamalaza Peninsula (Sofia region, northwest Madagascar). This is a transition zone between the Sambirano region in the north and the western dry deciduous forest region in the south. The forests in this area contain plant species typically found in dry forest as well as those from the wetter Sambirano domain (for example, various Dyospyros species, Garcinia pauciflora, Plagiocytus jumellei, Prociopsis hildebrandti, Stychnos madagascariensis, and Triilepisium madagascariensis; Birkshaw (2004)). Today, E. m. flavifrons is only found in a few remaining and already highly fragmented stretches of primary and secondary forest in an area of about 2,700 km² south of the Andranomalaza, north of the Maevvarano, and west of the Sandrakota rivers (Meyers et al. 1989; Rabarivola et al. 1991; Meier et al. 1996; Mittermeier et al. 2006). Schwitzer et al. (2005) estimated the E. m. flavifrons population of the Sahamalaza Peninsula to be between 2,780 and 6,950 individuals. Rakotondratsima (1999) stated that the population has shown a decline of 35.3% between 1996 and 1999, probably mainly due to habitat destruction (see also Andriamanandratra 1996). The underlying threat to E. m. flavifrons is the increasing pressure from human population expansion in Madagascar (Harcourt and Thornback 1990; Burney et al. 1997; Richard and O’Connor 1997; Andrianjakarivelo 2004), with an annual human population growth of 2.7% (Population Reference Bureau 2006, <http://www.prb.org>).

The blue-eyed black lemur was classified as Critically Endangered (A2cd) by the IUCN in 1993 and again in 2005.

To date, the ecology and behavior of the blue-eyed black lemur has neither been studied extensively in the wild nor in captivity, and the existing knowledge is thus either fragmented or anecdotal (Schwitzer and Kaumanns 2005).

Comparative studies of E. m. flavifrons living in habitats that differ in their degree of degradation might help to explain the ecological and behavioral flexibility of blue-eyed black lemurs. If E. m. flavifrons is a habitat generalist, as would be expected from studies of other Eulemur species, the lemurs should use primary and secondary forest similarly. If it is a habitat specialist, however, parameters such as population density and habitat use should differ in primary and secondary forests, and depending on varying degrees of human exploitation. Larger home ranges should be necessary for lemurs to find sufficient food resources in secondary, less suitable habitat if one assumes that home range size correlates with the distribution of food resources (Clutton-Brock and Harvey 1979; Robbins et al. 2006). In this study we describe differences in structural vegetation characteristics of a primary and a secondary forest fragment inhabited by different blue-eyed black lemur groups. We also compare the size and utilization of the groups’ home ranges, as well as the use of vertical forest strata. The results are extrapolated to compare the availability and diversity of potential feeding and sleeping trees for E. m. flavifrons within these fragments, and thus to assess the suitability of altered habitat for the species.

Methods

Study site

The study was conducted in the Ankarafo Forest, in the UN Biosphere Reserve and National Park on the Sahamalaza Peninsula, and part of the Province Autonome de Mahajanga, NW Madagascar. It extends between 13°52’S and 14°27’S and 45°38’E and 47°46’E (WCS/DEC 2002). The Ankarafo Forest includes primary and secondary forest fragments, which are believed to accommodate one of the largest connected populations of blue-eyed black lemurs (Schwitzer et al. 2005). There are no larger connected areas of intact primary forest left on the Sahamalaza Peninsula, and even the remaining fragments of primary forest all show some degree of anthropogenic disturbance and/or edge effects.

The climate is strongly seasonal, with a cool, dry season from May to October and a hot, rainy season from November to April. Mean annual precipitation is 1,600 mm, with the highest rainfall in January and February. Temperature fluctuates around 28.0°C throughout the year, with a maximum average temperature of 32.0°C (November) and a minimum average of 20.6°C (August).

Habitat structure and forest characteristics

The point-centered quarter method was used to describe the habitats used by four different groups of blue-eyed black lemurs living in a primary and a secondary forest fragment, respectively (Ganzhorn et al. 1997; Ganzhorn 2002, 2003).
The primary forest fragment measured 0.13 km², and the secondary forest fragment 0.48 km². The fragments were separated from each other by a stretch of less than 1 km of grass savannah and shrub. They were considered to be representative of the forest structure in general. Sixty sample points were taken in each of two forest fragments on parallel perpendicular lines located at intervals of 15 m on a 105-m transect line. Distances between sample points along the perpendicular lines were chosen randomly. Each sample point represented the centre of four compass directions that divided the sample plot into four quarters. In each quarter the distance from the centre to the nearest tree ≥ 3.1 cm DBH (diameter at breast height) was measured. Trees < 3.1 cm DBH were not considered as being used by the lemurs and were therefore not measured. Altogether, 480 trees were sampled. Tree density per unit area (A = 10,000 m²) was then calculated as $Aid^2$, where $d$ is the mean distance between the trees and the centre of the associated sample point.

Medians and upper and lower quartiles were calculated for DBH, tree height, crown diameter and height of the first branch in both forest fragments. We estimated the percentage of closure of the overstorey for each sample point by assigning the covered area on a photo taken from the ground to one of the following five categories: full closure, $\frac{3}{4}$ closure, $\frac{1}{2}$ closure, $\frac{1}{4}$ closure, fully open. Because trees with lianas may be preferred as sleeping sites by lemurs (Rendigs et al. 2003), we also estimated the proportion of trees without lianas, with a single, or with several lianas growing up to the tree crown. As a measure of recent anthropogenic disturbance of the forest fragments, we noted the number of tree stumps visible from each sample point.

To compare the availability of larger food and resting trees (that could support an entire group of lemurs at the same time) in the primary and secondary forest fragments, we determined the minimum DBH of trees used for feeding and resting. Food and resting trees were defined as such trees supporting ≥ 3 lemurs at the same time for at least 10 consecutive minutes, and were recorded regularly throughout the year. The minimum DBH for food or resting trees across both forest fragments was ≥ 22.47 cm.

For further classification of the forest fragments, we collected herbarium specimens from each of the 480 trees sampled with the point-centered quarter method. The specimens were taken simultaneously with the measurements. In addition to the trees ≥ 3.1 cm DBH, specimens from trees < 3.1 cm DBH were also taken in order to obtain a comprehensive picture of forest composition. A total 960 specimens were collected in the two forest fragments. They were identified with the help of the botanical department of the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo.

**Habitat use**

Four groups of *E. m. flavifrons* in two different fragments of the Ankavaram Forest (see above) were each followed for 24 hour/month during eight months between July 2004 and July 2005, combined resulting in 600 h of observation spanning the dry and the rainy seasons. The two fragments consisted mainly of primary and secondary vegetation respectively.

Activity data and data on home range use were collected by recording the activity and position that all or most members of the respective group were engaged in at two-minute intervals (Altman 1974; Mann 1999, 2000). To determine the vertical position of the lemurs, the forest was classified into four different vertical levels: ground; subcanopy (trees or shrubs which extend between the ground and the lowest areas of the canopy); understorey (trees representing the lower part of the canopy); and overstorey (trees representing the upper part of the canopy and emergents).

**Forest cover and home range size**

Primary and secondary forest fragments were divided by an area which is only covered with grass savannah, bushes and shrubs. The secondary forest within the study area was considered to be at least 35 years old, based on aerial and satellite images and GIS data obtained from Conservation International. Limits of the forest fragments were recorded via GPS, and included forest as well as shrubs.

To determine the horizontal position of the animals, all food and resting trees used by a lemur group were marked and recorded via GPS (for definition of food and resting trees see above). We then superimposed 10 × 10 m squares on a map around the marked trees to take their crown diameters into account. Home range size was calculated using the minimum convex-polygon method (Hayne 1949), connecting the outer edges of the extremity squares and measuring the total area enclosed. GPS data were analyzed with ArcGIS 9* and ArcView® (ESRI 2005). To allow for analysis of seasonal changes in home range size we lumped the data for the two lemur groups in each forest fragment, respectively.

**Statistics**

The units of statistical analysis used to test for differences in habitat structure and forest characteristics between the primary and the secondary forest fragment were either the total number of trees and shrubs sampled (n = 480 trees + 480 shrubs) or the number of point-centered plots (n = 120). The nonparametric Mann-Whitney ‘U’ test and the Chi-Square test were applied to these data. For analyzing differences in plant composition between both types of forest, we used the total number of all trees that could be identified to species level (n = 832) as statistical units, and applied a ‘G’ test. To analyze the use of plant families by the lemurs in primary and secondary forest, we used data on trees that were used by the animals and that could be identified to species level as statistical units (n = 58), and applied a ‘G’ test. To test for differences in the use of feeding and resting trees, we applied a ‘G’ test to the total number of regularly used trees (n = 134). Data were analyzed using the software SPSS 14.0 (Statsoft, 2005) and SSS 1.1m (Rubisoft, 2002).
Results

Habitat structure and forest characteristics

The structural comparison of the two habitat types revealed differences in structural variables (Table 1) as well as in plant diversity and plant communities. Differences were significant for trees ≥3.1 cm DBH (Mann-Whitney ‘U’ test: p≤0.01; two-tailed; Z = -6.457), which occurred in higher densities in the secondary forest fragment and for potential food or resting trees, usable for a whole group of lemurs (≥22.47 cm DBH), which were more abundant in the primary forest fragment (primary forest = 39 trees; secondary forest = 12 trees; Chi-Square test: n = 480; p≤0.01). Median DBH of measured trees and the number of trees with lianas were significantly greater in the primary than in the secondary forest fragment (Median DBH: Mann-Whitney ‘U’ test: p≤0.01; two-tailed; Z = -12.311 and number of trees with lianas: Mann-Whitney ‘U’ test: p≤0.01; two-tailed; Z = -4.956).

Table 2 shows the plant composition and the proportion of different plant families in the two forest fragments. Twenty-two plant families occurred in both the primary and secondary forests, 20 occurred only in the primary, and 12 only in the secondary forest. The number of different plant families was significantly higher in primary forest (42 versus 34; ‘G’ test: p≤0.05). The two fragments also differed considerably with regard to their plant communities (Table 2).

Habitat use

The lemurs in the primary forest fragment spent most of their time in the highest forest strata, but in the secondary forest fragment the overstorey was less used than the understory (Fig. 1). All levels, except for the ground, varied in their degree of use by the lemurs over the course of the year. However, the distribution of forest level use over the year appears to be more even in primary than in secondary forest habitat. This becomes evident by looking at the more frequent use of the lower forest strata in secondary forest during the dry season (Figs. 2a and 2b).

The forest floor was only irregularly used and, if used at all, the lemurs normally only stayed on the ground for seconds at a time (twice in October, once in November and once in December). During the dry season, in June, an infant male was observed on the ground for several minutes, drinking from a puddle.

Use of plant families

Thirty-five of 97 regularly-used trees, belonging to 17 plant families, were individually identified in primary forest, and 23 out of 37 regularly used trees, belonging to six plant families, in secondary forest. The family-level diversity was thus higher in trees used by the lemurs in primary forest than in trees used in secondary forest (‘G’ test: p≤0.01). In

![Figure 1. Forest level use by Eulemur m. flavifrons in primary and secondary forest during the study period (% of observation time). Levels: ground; subcanopy, extending between the ground and the lowest areas of the canopy; understory, representing the lower part of the canopy; overstorey, representing the upper part of the canopy and emergents.](https://bioone.org/journals/Primate-Conservation/article-pdf/1/4/82/5181625/82.pdf)
Habitat use of *E. m. flavifrons* in forest fragments

In this study we examined the use of two different forest fragments by *Eulemur macaco flavifrons*, one of which was predominantly primary forest, and the other secondary. The latter was in the process of regeneration after significant human disturbance of the original forest vegetation over an extended period in the past. It displayed major differences in forest structure and canopy species composition as compared to the nearby primary forest. All conditions for the definition of secondary forest given by Chokkalingam and de Jong (2001) were met in this study fragment.

The two fragments differed considerably in a number of variables. The primary forest fragment had more trees with lianas, which provided additional cover for the lemurs and were thus potential sleeping trees (Rendigs et al. 2003). It also had more large trees (DBH ≥22.47 cm). Also, overall plant biodiversity was higher in the primary than in the secondary forest fragment. Moreover, plant communities were different in the two fragments. Nevertheless, human pressure was higher and canopy cover altogether less dense in the primary forest fragment (Table 1), which means that at the time of our study, it was showing some degree of disturbance. Despite this, our results clearly demonstrate differences in habitat use of *E. m. flavifrons* in the primary and secondary forest fragment.

While the animals in primary forest spent most of their time in the highest forest strata in all months of the year, in secondary forest the patchily distributed overstorey was almost unused during the stormy dry season. During June, July and August, a strong wind from the south-east to the north-west (*Varatraza*) dominates the weather in the study area. At this time, blue-eyed black lemurs decreased their activity (Schwitzer et al. submitted) and spent most of the day in the largest

**Table 2.** Plant community composition in the two forest fragments.

<table>
<thead>
<tr>
<th>Trees</th>
<th><strong>Primary forest [%]</strong> N=240</th>
<th><strong>Secondary forest [%]</strong> N=240</th>
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<td>0.45</td>
</tr>
<tr>
<td>Chrysobalanaceae**</td>
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</tr>
<tr>
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<td>0.45</td>
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</table>

*Only in primary forest; **only in secondary forest.

**Use of trees for feeding and resting**

In each type of forest, some trees were used by the lemurs exclusively for resting and others for both, feeding and resting. In the primary forest fragment, *E. m. flavifrons* used significantly more trees coevally for feeding and resting (*G* test: n = 134; p<0.05) than in secondary forest (Fig. 3).

**Forest cover and home range size**

The total home ranges of the four study groups differed greatly in size and covered between 3.8 ha (primary forest) and 19.6 ha (secondary forest). Home ranges of neighboring groups overlapped in both types of forest (Fig. 4). Home range size changed during the dry and the rainy season in both types of forest. They were smaller during the dry season. In secondary forest the animals decreased the size of their home range to 1.4 ha (9.7% of the original home range size), and in primary forest to 5.7 ha (77.4% of the original home range size) during the dry season (Fig. 5).

**Discussion**

In this study we examined the use of two different forest fragments by *Eulemur macaco flavifrons*, one of which was predominantly primary forest, and the other secondary. The latter was in the process of regeneration after significant human disturbance of the original forest vegetation over an extended period in the past. It displayed major differences in forest structure and canopy species composition as compared to the nearby primary forest. All conditions for the definition of secondary forest given by Chokkalingam and de Jong (2001) were met in this study fragment.

The two fragments differed considerably in a number of variables. The primary forest fragment had more trees with lianas, which provided additional cover for the lemurs and were thus potential sleeping trees (Rendigs et al. 2003). It also had more large trees (DBH ≥22.47 cm). Also, overall plant biodiversity was higher in the primary than in the secondary forest fragment. Moreover, plant communities were different in the two fragments. Nevertheless, human pressure was higher and canopy cover altogether less dense in the primary forest fragment (Table 1), which means that at the time of our study, it was showing some degree of disturbance. Despite this, our results clearly demonstrate differences in habitat use of *E. m. flavifrons* in the primary and secondary forest fragment.
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trees, hiding on branches near the trunk. Groups of massive trees seem to be necessary for providing sufficient protection for the lemurs on the Sahamalaza Peninsula during the Varatraza months. The overstorey of the secondary forest may provide insufficient cover from aerial predators in the dry season, when some of the trees do not have leaves. In addition to large trees, the primary forest fragment had a greater diversity of families of trees, and more trees that served as food and resting trees, allowing for shorter travel distances for the animals. The combination of these factors might be responsible for our finding that the home range size of *E. m. flavifrons* was smaller in primary forest. Moreover, the density of blue-eyed black lemurs was higher in primary forest than in secondary forest (Schwitzer et al. 2005).

This is consistent with the findings of Wilson et al. (1989), who sighted *Eulemur coronatus* in primary forest much more frequently, and in greater numbers, than in edge or degraded forest. Overdorff (1992) related that *Eulemur rufus* and *Eulemur rubriventer* preferred the highest forest strata, and Ganzhorn and Schmidt (1998) found that *Microcebus murinus* reached lower population densities in secondary than in primary forest (see also Ganzhorn et al. 1996; Smith et al. 1997). Studies on South American howler monkeys (genus *Alouatta*) in Nicaragua demonstrated a marked preference for primary forest habitats, presumably due to a higher density of food species (McCann et al., 2003). Group size and density of howler monkeys appeared to be smaller where there was a higher degree of human-modified habitat (McCann et al. 2003; Rodriguez-Toledo et al. 2003). Estrada and Coates-Estrada (1995) found a greater primate presence in undisturbed forest fragments where vegetation was taller than in fragments where the canopy height was lower than 10 m.

The blue-eyed black lemurs were expected to be habitat generalists with a broad habitat tolerance, probably because they were previously classified as frugivorous and adaptable (Andriamanandratra 1996; Rakotondratsima 1999). Nevertheless, our study indicates that they show some degree of habitat selectivity. The lack of large trees and lianas as well as the lower number of different plant families may have lead to a decrease in the density of blue-eyed black lemurs in secondary forest fragments, as reported by Schwitzer et al. (2005). This indicates that secondary forests might be of only limited value in providing a suitable habitat for the species, even though it is there that they can exploit food trees such as mango, *Mangifera indica*. Long-term studies in secondary forest are needed in order to see if blue-eyed black lemur populations are viable in areas entirely lacking primary forest.

*Eulemur m. flavifrons* was classified as Critically Endangered (CR A2cd) in the most recent IUCN Red List assessment on the basis of a habitat loss of 80% during the last 25 years. Its remaining habitat is already substantially fragmented (Schwitzer et al. 2005). The main goal for future conservation plans in Sahamalaza should therefore be the protection of the remaining patches of primary forest, using secondary forest as buffer zones and corridors between primary forest blocks.

**Conclusions**

Blue-eyed black lemur groups are able to adapt to different types of habitat. Home range size and use differ between primary and secondary forest fragments. *Eulemur m. flavifrons*...
groups have larger home ranges and lower densities in secondary forest compared to primary forest, suggesting that the former is less suitable. Different forest types evidently differ in their suitability for *Eulemur macaco flavifrons*, which, as such, cannot be classified as a habitat generalist. Long-term studies in isolated secondary forest and forest-agricultural mosaic fragments need to be carried out to reveal whether or not blue-eyed black lemurs can survive without access to primary forest.

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