Ecological flexibility as measured by the use of pioneer and exotic plants in two lemurids: 

\textit{Eulemur collaris} and \textit{Hapalemur meridionalis} 

\textbf{Short title:} Do lemurid diets shape ecological flexibilities?

\textbf{Keywords:} pioneer species; exotic plants; edge habitat; collared brown lemur; southern bamboo lemur; Madagascar

\textbf{Abstract}

Primate responses to habitat alteration vary depending on the species’ dietary guild and forest type. Leaves from secondary vegetation can provide nutritious resources to folivorous primates, whereas frugivores, burdened with a scattered spatial and temporal distribution of fruiting resources, require larger home ranges, potentially limiting their ability to cope with altered landscapes. Within coastal south-eastern Madagascar, we sought to determine whether two lemur species occupying contrasting ecological niches (i.e., dietary guilds) respond differently to the changing features of their degraded and fragmented habitat. We conducted behavioural observations between 2011 and 2013 on frugivorous collared brown lemurs (\textit{Eulemur collaris}) and folivorous southern bamboo lemurs (\textit{Hapalemur meridionalis}). In order to estimate the ability of lemurs to use pioneer species, we categorised all plants used for feeding and resting as either ‘fast-growing’, ‘mid-growing’, or ‘slow-growing’. We fitted linear mixed-effects models, one for each plant growth category with monthly proportional use rates as the dependent variable, and included species (\textit{E. collaris} and \textit{H. meridionalis}), activity (feeding and resting), and season (dry and wet) as fixed effects. Our results show that \textit{E. collaris} used both
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slow- and mid-growing plant species most often, while *H. meridionalis* were more likely to use fast-growing plants, which indicated an ability to utilise secondary/disturbed vegetation. Frugivorous *E. collaris* appear more limited by climax plants, while folivorous *H. meridionalis* appear to be slightly more adaptable, a finding that is consistent with other primate folivores.

**Introduction**

Tropical deforestation is one of the primary threats to global biodiversity (Achard et al. 2002; Asner et al. 2009; Dirzo and Raven 2003; Gibson et al. 2011; Sala et al. 2000). The destruction, fragmentation, and degradation of remaining habitats threaten many species’ ability to survive (Oates 2013). While forest fragments typically persist after deforestation, they effectively become islands within an anthropogenic landscape, most of which are unsuitable habitat for the majority of forest species (Broadbent et al. 2008; Laurance et al. 2009, 2011).

Ecological flexibility is loosely defined as the ability of an organism to adjust to changes, e.g., anthropogenic, gradual, and stochastic, within its environment (Isaac and Cowlishaw 2004; Nowak and Lee 2013; Wieczkowski 2003). In more specific terms, *flexibility* may encapsulate various behavioural modifications including the diet, i.e., exploitation of alternative food sources, as well as altering activity, ranging pattern and vertical strata use in response to new dietary opportunities. This ability to expand niche breadth is key to withstanding the risks of anthropogenic and/or stochastic habitat modification (Lee 2003).

It is important to understand behavioural responses of forest dwelling primates to habitat degradation and fragmentation due to the increasing rate of habitat alteration and limited ability of most species to move between forest fragments (Marsh 2003). How a primate responds to habitat degradation, however, seems to vary depending on species and type of forest (Chapman...
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may produce foods of higher dietary quality compared to foods available in mature forests, thus
making folivorous (i.e., leaf-eating) primates less affected by habitat degradation (Chapman et al.
2002; Ganzhorn 1995; Ganzhorn et al. 1999b; Plumptre and Reynolds 1994). For example,
populations of folivorous black howler monkeys (*Alouatta caraya* and *A. pigra*), have been
documented to use and rely heavily on fast-growing, exotic plant species (e.g., *Eucalyptus* and
shaded cocoa plantations) for both occasional food and resting/sleeping within fragmented,
anthropogenic landscapes (Bicca-Marques and Calegaro-Marques 1994; Bonilla-Sánchez et al.
2012; Zárate et al. 2014). Similarly, black-and-white colobus (*Colobus guereza*) appear to do
well in some disturbed (i.e., previously logged) habitats (Chapman et al. 2000; Tutin et al.
1997b). Frugivorous (i.e., fruit-eating) primates, however, have to cope with the scattered spatial
and temporal distribution of fruiting resources, thus often requiring larger home ranges (Estrada
and Coates-Estrada 1996; Rode et al. 2006; but see Tutin et al. 1997a). Many frugivorous
primates avoid forest fragments, e.g., grey-cheeked mangabeys (*Lophocebus albigena*) and
Mexican spider monkeys (*Ateles geoffroyi vellerosus*), and appear to be restricted to continuous
forests (Estrada and Coates-Estrada 1996; Tutin et al. 1997b). Despite these potential limitations,
some frugivorous primates, such as chimpanzees (*Pan troglodytes*) and Sumatran orangutans
(*Pongo abelii*), demonstrate an ability to survive within degraded, anthropogenic landscapes,
foraging on a mixture of crops and wild fruits (Campbell-Smith et al. 2011; Hockings and
McLennan 2012; McLennan and Hockings 2014). As frugivorous primates are important seed
dispersers, their ability to cope within anthropogenic landscapes has major implications for the
maintenance of forest diversity: they are fundamental in the regeneration of degraded habitats
(Chapman 1995; Ganzhorn 1995; Razafindratsima and Dunham 2014).
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On a global scale, frugivorous strepsirrhines from Madagascar contribute on a larger scale to their respective ecosystems, e.g., seed dispersal, compared to primates in the Neotropics or mainland Africa (Jernvall and Wright 1998). As frugivorous lemurs are essential to maintaining the unique forests of Madagascar, their demise would likely trigger extinction cascades (Federman et al. 2016; Ganzhorn et al. 1999a; Jernvall and Wright 1998; Razafindratsima and Dunham 2014). Within Madagascar, for example, greater than 80% of forest area exists less than 1 kilometre from an edge (Harper et al. 2007), and thus fragmentation is of great concern for the survival of forest fauna and flora species (Hannah et al. 2008; Waeber et al. 2015). This can be further complicated by introduced exotic and invasive species that threaten the preservation of endemic biodiversity as well as ecosystem restoration efforts (Braithwaite et al. 1989; D’Antonio and Vitousek 1992). While the limits of lemurs’ tolerance, i.e., coping strategies, to fragmented, secondary, and degraded habitats are poorly understood (Campera et al. 2014; Donati et al. 2011; Eppley et al. 2015a; Gardner 2009; Irwin et al. 2010; Lehman et al. 2006), it is imperative to understand the relationship between species and these altered habitats if we are to properly conserve primates and other species (Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Isabirye-Basuta and Lwanga 2008; Onderdonk and Chapman 2000).

The Anosy region along the southeast coast of Madagascar provides a complex mosaic of heavily fragmented upland and swamp forest habitats, mono-dominant exotic species, old and new timber plantations, and a large-scale ilmenite ore mine and separation plant facility (Barthlott et al. 1996; Ramanamanjato et al. 2002; Ganzhorn et al. 2007b). This area provides an excellent model with which to explore the behavioural and feeding ecological flexibilities amongst the lemurs which inhabit it (Bollen and Donati 2006; Eppley et al. 2015a;
Rabenantoandro et al. 2007), and how they cope with habitat disturbance. Within southeast Madagascar, sympatric collared brown lemur (*Eulemur collaris*) and southern bamboo lemur (*Hapalemur meridionalis*) occupy different ecological niches, the frugivorous and folivorous dietary guild, respectively. Previous research has shown that *E. collaris* is tolerant to habitat degradation and strong seasonal resource availability by flexibly modifying many aspects of its behavioural ecology, such as feeding strategies and home range use (Campera et al. 2014; Donati et al. 2011). Similarly, *H. meridionalis* display a flexible ecology, utilising three distinct habitats (littoral forest, littoral swamp, and *Melaleuca*-dominated swamp) for both resting and feeding purposes (Eppley et al. 2015a).

While the use of disturbed habitats by these two lemurids has been increasingly documented (Campera et al. 2014; Eppley et al. 2015a), our study sought to contrast the two taxa and specifically determine to what extent their ecological flexibility played a role in their ability to use altered and degraded habitats. Habitat edges often contain a higher abundance of pioneer, i.e., fast-growing, species as compared to climax habitat (Laurance et al. 2006, 2007). Furthermore, climax, i.e., slow-growing, plants struggle to regenerate in open habitats as is very often the case in edge areas and/or plantations (Benitez-Malvido 1998). The general observation that folivores are able to cope better within degraded environments led us to predict that *H. meridionalis* will use more forest edge habitat compared to *E. collaris*. In terms of utilising plant species as feeding and/or resting resources, we sought to determine whether the dietary guilds of our two taxa are predictive of an ability to use fast growing plant species, typically represented by pioneer species, and how this is a potential signal of ecological flexibility to altered habitats. As fast-growing tropical plant species often provide a continuous (i.e., non-seasonal) and relatively large biomass presence of young leaves (Coley et al. 1985; Poorter 1999), which
consequently produce more protein (Wasserman and Chapman 2003), we predict that *H. meridionalis* will use fast-growing tree species more often than sympatric frugivorous *E. collaris*. Due to the contrasting dietary guilds of our two study species, we predict that there will be little overlap in feeding resources. As these are the two largest lemur species within the southeast coastal landscape, however, we predict that they will use similar tree species for resting, as this degraded littoral environment has a limited number of mature trees. We expect the largest differences in feeding tree use to be evident for *E. collaris* during the dry season, i.e., when there are fewer available food resources (Bollen and Donati 2005; Campera et al. 2014). Lastly, exotic plant species (e.g., introduced, non-endemic), are shown to incur lower levels of leaf herbivory compared to endemic plant species (Lake and Leishman 2004). Thus, we predict that the folivorous *H. meridionalis* would avoid exotic plant species.

**Methods**

**Study site**

We conducted our study in the Mandena Conservation Zone (24°95’S 46°99’E; hereafter Mandena), along the southeast coast of Madagascar, approximately 10 km north of Fort-Dauphin (Tolagnaro). Located within three kilometres of the coast and characterized by a low canopy growing on sandy substrate (Dumetz 1999), this protected area consists of approximately 82 ha of seasonally inundated swamp among 148 ha of degraded littoral forest fragments (Ganzhorn et al. 2007a). This littoral zone experiences less seasonality than the humid eastern forests (Bollen and Donati 2005), with a mean temperature of 22.5°C (range: 9.5 – 35.0°C) and total annual precipitation of 2,808mm, typically generating a wet season between November and April (Eppley et al. 2015a, 2016b). Compared to the less degraded littoral forests further north (Bollen
and Donati, 2006), the degree of anthropogenic degradation in Mandena resulted from the historical extraction of utilitarian timber species and charcoal production due to the close proximity of the Anosy region capital (Ingram and Dawson 2006; Vincelette et al. 2007b). The area immediately surrounding these fragmented forests is composed of mono-dominant timber plantations, an exposed sand-scrub matrix, and the large-scale ilmenite mining concession and associated administration and extraction/separation facilities (Ganzhorn et al. 2007b). In addition to the two cathemeral lemurids, i.e., *E. collaris* and *H. meridionalis*, this littoral area is inhabited by four nocturnal strepsirrhines: Ganzhorn’s mouse lemur (*Microcebus ganzhorni*), eastern fat-tailed dwarf lemur (*Cheirogaleus medius*), greater dwarf lemur (*C. major*), and the southern woolly lemur (*Avahi meridionalis*).

**Study species**

Our study focuses on two sympatric lemur species inhabiting Mandena: *E. collaris* and *H. meridionalis*. Both are medium-sized lemurs, although *E. collaris* is considerably larger, with a mean body mass of 2.2 kg (Donati et al. 2011), compared to the mean body mass of *H. meridionalis* which is 1.1 kg (Eppley et al. 2015b). Both of these lemurid species exhibit a cathemeral activity pattern (Donati et al. 2007; Eppley et al. 2015c). Species are classified according to dietary guild based on diets comprising ≥50% of a specific food category (Ganzhorn 1997). As the annual diet of *E. collaris* consists of ≥70% fruits, it is classified as frugivorous (Donati et al. 2007, 2011). The annual diet of *H. meridionalis* consists of ≥70% foliose matter, thus this species is classified as folivorous (Eppley et al. 2011, 2016a).

We captured lemur subjects via Telinject® blow darts (administered by an experienced Malagasy technician) containing a hypnotic anaesthesia (4-5 mg/kg of ketamine hydrochloride or
tiletamine hydrochloride. Four individuals (one for each group) of *E. collaris* were captured and equipped with radio-collars (TW-3, Biotrack, 29 g). We captured ten individuals of *H. meridionalis* from four social groups, and radio-collared with data-logging tags (ARC400, Advanced Telemetry Systems, Inc.; Isanti, MN, USA). We utilised radio-collars to expedite the amount of time it took to locate lemur groups each day; however, not all adult focal individuals were radio-collared. All subjects recovered from anaesthesia within 1.5 h and were not moved from the capture area. Furthermore, we followed lemurs until they regained full mobility in trees. There were no injuries as a consequence of the captures. The collars were below the 5% threshold of the subjects’ weight. For more specific information on the capturing/collaring processes of *E. collaris*, see Campera et al. (2014), and for *H. meridionalis*, see Eppley et al. (2015c, 2016c).

Data collection

We collected data for each species during different years. For *E. collaris*, MB and MC observed group AB from March 2011 to January 2012, and group C from June 2011 to January 2012. Data collection was conducted on a focal individual from 06:00 to 18:00 h. We collected behavioural data in 5 min intervals via instantaneous sampling (Altmann 1974), specifically noting the tree species used for feeding and resting. Furthermore, we recorded the position of the focal *E. collaris* individual in 30 min intervals via a handheld GPS. For *H. meridionalis*, TME conducted full-day focal observations (from sunrise to sunset) with groups 1, 2, and 4 (we used group 3 exclusively for home range data collection) between January and December 2013. We identified all observed plant food items consumed by the focal individual, noting the plant species’ scientific name, and recorded feeding duration via continuous sampling (Altmann...
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Furthermore, we recorded all instances ≥ 15 min for continuous resting. Lastly, we recorded *H. meridionalis* focal waypoint locations via GPS in 15 min intervals.

JR and FR identified all plant species used for feeding and resting by both lemur species, and we categorized these into three successive growth rates as they occur under natural conditions. As such, *fast-growing* plant species reached maturity < 2 years, *mid-growing* plant species reached maturity between 2 – 5 years, while *slow-growing* species reached maturity in > 5 years, with categories based on previous botanical assessments (cf. Vincelette et al. 2007a).

Furthermore, JR identified exotic plant species (i.e., non-endemic), which we validated with an index of exotic and invasive species in Madagascar (Gérard et al. 2015).

Ethical Note

Our research protocols were approved and permits authorized by the Commission Tripartite of the Direction des Eaux et Forêts de Madagascar (Autorisation de Recherché n.29/11/MEF/ SG/DGF/DCB.SAP/SCB du 20/01/11 and n.240/12/MEF/SG/DGF/DCB.SAP/SCB du 17/09/12), adhering to the legal requirements of Madagascar. We conducted research under the collaboration agreement between the Department of Animal Biology of the University of Antananarivo and the Department of Animal Ecology and Conservation of the University of Hamburg, and QIT Madagascar Minerals (QMM).

Data analyses

We entered all ranging data into ArcGIS 10.2 (ESRI) using the Geospatial Modelling Environment (GME) spatial ecology interface (Beyer 2012). Ranging and statistical analyses were conducted using R statistical software version 3.2.3 (R Development Core Team 2015).
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determined each group home range with a 95% kernel density estimate, while core areas were
determined as a 50% kernel density estimate (Worton 1989). We then created a forest edge
polygon buffer 100 m inside the littoral forest boundary which allowed us to calculate the total
amount of forest edge and non-edge habitat within each lemur species’ home range and core
areas within Mandena (Laurance et al. 2007; Lehman et al. 2006).

From our behavioural sampling of *E. collaris* and *H. meridionalis*, we calculated monthly
proportional utilisation rates for all feeding and resting trees. For each of the three plant species
growth categorizations, we fitted General Linear Mixed-effects Models (LMM) using the lmer
function of the lme4 package developed for R (Bates et al. 2012). For each LMM, our dependent
response variable was the monthly proportion of plant species used (i.e., fast-growing plants,
mid-growing plants, and slow-growing plants), while our fixed effects were the lemur species (*E.
collaris* and *H. meridionalis*), activity (feeding and resting), and season (dry and wet). We
included lemur social group as random effect to control for repeated sampling. We then used the
ANOVA function to calculate likelihood ratio tests for model comparison, allowing us to
determine which model had the best explanatory power by comparing Akaike’s Information
Criterion (AIC) values for all possible models. *P*-values were obtained with a likelihood ratio
test using the afex package (Singmann 2014) developed for R, with significance considered at *P*
< 0.05. Residuals from the analyses did not deviate from normality according to the
Kolmogorov-Smirnov test.

To determine which factors are linked to the utilisation of exotic plants within Mandena,
we fitted Generalized Linear Mixed-effects Models (GLMM) using the glmer function of the
lme4 package developed for R (Bates et al. 2012), with the monthly use of an exotic plant as a
binomial dependent variable, as opposed to endemic plants. As with the LMMs, our fixed effects
were lemur species, activity, and season, with group included as random effect to control for repeated sampling. We then used the ANOVA function to calculate likelihood ratio tests for model comparison and determined which model had the most explanatory power by comparing the AIC values for all possible models.

Results

Ranging

We observed *E. collaris* for 962 h, while *H. meridionalis* were observed for 1,762 h. Both lemurid species’ home ranges were within the central to northern portions of Mandena, and were not limited to only littoral forest areas, but rather encompassed a mixture of both littoral forest and swamp (Fig. 1). Considering species’ home ranges, *E. collaris* used considerably larger areas than *H. meridionalis* (Table 1). The proportion of edge habitat used by both species within their home range were similar, with forest edge comprising a mean of 37.4% of *E. collaris* home ranges (N = 2), and 45.6% of *H. meridionalis* home ranges (N = 4) (Table 1). Considering only the core areas, forest edge comprised similar mean percentages of *E. collaris* (50.6%) and *H. meridionalis* (42.6%) habitat.
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**Fig. 1.** Location of *E. collaris* and *H. meridionalis* group home ranges (95% kernel density estimates) within the Mandena littoral forest and swamp. Portions of the swamp are composed of mono-dominant strands of exotic *Melaleuca*, while lighter grey areas to the east are a sand-scrub matrix and those to the west are a matrix of sand-scrub and Eucalyptus plantations. Data on *E. collaris* were collected between March 2011 and January 2012, and *H. meridionalis* between January and December 2013.

**Table 1.** Area (in hectares) of both home range (95% kernel density estimate) and core area (50% kernel density estimate) for *E. collaris* and *H. meridionalis* groups in Mandena. Edge habitat was calculated as the area (ha) within 100 m buffer from the forest edge. Data were collected on *E. collaris* between March 2011 and January 2012, and on *H. meridionalis* between January and December 2013.

<table>
<thead>
<tr>
<th>Species</th>
<th>Group</th>
<th>Months of observation</th>
<th>Home range (ha)</th>
<th>Core area (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. collaris</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Home range (ha)</td>
<td>Core area (ha)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Edge (ha)</td>
<td>Edge (%)</td>
</tr>
<tr>
<td>AB</td>
<td>11</td>
<td>41.16</td>
<td>19.07</td>
<td>46.33</td>
</tr>
<tr>
<td>C</td>
<td>8</td>
<td>83.32</td>
<td>23.68</td>
<td>28.42</td>
</tr>
<tr>
<td><em>H. meridionalis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>12</td>
<td>18.39</td>
<td>8.40</td>
<td>45.68</td>
</tr>
<tr>
<td>2</td>
<td>12</td>
<td>17.66</td>
<td>9.75</td>
<td>55.21</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
<td>6.60</td>
<td>3.65</td>
<td>55.30</td>
</tr>
<tr>
<td>4</td>
<td>12</td>
<td>10.43</td>
<td>2.75</td>
<td>26.37</td>
</tr>
</tbody>
</table>
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We identified 105 different plant species used by *E. collaris* and 112 species used by *H. meridionalis* for feeding and resting (Table 2). Twenty-four plant species were eaten by both lemurs. More specifically, *E. collaris* food resources comprised 16.9% fast-growing, 28.6% mid-growing, and 54.6% slow-growing plants. For *H. meridionalis*, food resources comprised 38.0% fast-growing, 16.9% mid-growing, and 45.1% slow-growing plants. Twenty-seven plant species were used for resting by both lemur species. For *E. collaris*, we categorized 14.3% of all resting plants as fast-growing, 24.8% as mid-growing, and 61.0% as slow-growing, while for *H. meridionalis*, we categorized 27.7% of their used plants as fast-growing, 14.3% as mid-growing, and 58.0% as slow-growing. Both *E. collaris* and *H. meridionalis* displayed large differences in their utilisation of these plant growth categories between activity (Fig. 2) and season (Fig. 3).

Table 2. Number of species within feeding and resting plant species’ growth categorization for *E. collaris* (March 2011 to January 2012) and *H. meridionalis* (January to December 2013) in Mandena.

<table>
<thead>
<tr>
<th>Plant categories</th>
<th><em>E. collaris</em></th>
<th><em>H. meridionalis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Feed</td>
<td>Rest</td>
</tr>
<tr>
<td>Fast-growing</td>
<td>13</td>
<td>2</td>
</tr>
<tr>
<td>Mid-growing</td>
<td>22</td>
<td>11</td>
</tr>
<tr>
<td>Slow-growing</td>
<td>42</td>
<td>43</td>
</tr>
</tbody>
</table>

Note: *E. collaris* also relied on six unidentified plant species that were not included in the analyses.
Fig. 2. Comparison of monthly proportional medians (including interquartiles and ranges) between *E. collaris* and *H. meridionalis* on their selection of (a) fast-growing, (b) mid-growing, and (c) slow-growing plants for feeding and resting. Data were collected between March 2011 and January 2012 on *E. collaris*, and between January and December 2013 on *H. meridionalis*. 
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Fig. 3. Comparison of monthly proportional medians (including interquartiles and ranges) between *E. collaris* and *H. meridionalis* on their selection of (a) fast-growing, (b) mid-growing, and (c) slow-growing plants during the dry and wet seasons. Data were collected between March 2011 and January 2012 on *E. collaris*, and between January and December 2013 on *H. meridionalis*. 
The model with the best predictive value for fast-growing plants (AIC = -93.06, $\chi^2 = 21.59$, $df = 1$, $P < 0.001$) showed that both lemur species and activity were likely to influence their use (Table 3) while season had no effect. Specifically, fast-growing plants were most likely to be used by *H. meridionalis*, and most often for feeding (Fig. 2a). Season was not significantly predictive (Fig. 3a). The model with the best predictive value for mid-growing plants (AIC = -163.11, $\chi^2 = 9.29$, $df = 1$, $P < 0.01$) showed that all fixed-effects, i.e., species, activity, and season, influenced use of these plants (Table 3). Specifically, *E. collaris* was most likely to use mid-growing plants. Furthermore, these plants were more likely to be used for feeding (Fig. 2b), and to be used in the dry season (Fig. 3b). The model with the best predictive value for slow-growing plants (AIC = -63.90, $\chi^2 = 21.87$, $df = 1$, $P < 0.001$) showed again that all fixed-effects, i.e., species, activity, and season, influenced use of these plants (Table 3). *E. collaris* was most likely to use slow-growing plants, with these plants most often used for resting (Fig. 2c), specifically during the wet season (Fig. 3c).
Table 3. Linear mixed models predicting increased monthly proportion of using fast-growing plants, mid-growing plants, and slow-growing plants by *E. collaris* and *H. meridionalis* in Mandena, Madagascar. Data were collected between March 2011 and January 2012 on *E. collaris*, and between January and December 2013 on *H. meridionalis*.

<table>
<thead>
<tr>
<th>Growth class</th>
<th>Variable</th>
<th>$\beta$</th>
<th>SE</th>
<th>95% CI</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fast-growing</td>
<td>Intercept</td>
<td>0.13</td>
<td>0.04</td>
<td>0.06, 0.21</td>
<td>3.42</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>0.41</td>
<td>0.42</td>
<td>0.33, 0.49</td>
<td>9.78</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Activity</td>
<td>-0.19</td>
<td>0.29</td>
<td>-0.25, -0.14</td>
<td>-6.66</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Season</td>
<td>-0.02</td>
<td>0.03</td>
<td>-0.08, 0.03</td>
<td>-0.85</td>
<td>0.39</td>
</tr>
<tr>
<td>Mid-growing</td>
<td>Group</td>
<td>Variance</td>
<td>0.03</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>Variance</td>
<td>0.15</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slow-growing</td>
<td>Intercept</td>
<td>0.55</td>
<td>0.04</td>
<td>0.48, 0.63</td>
<td>14.86</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>-0.29</td>
<td>0.04</td>
<td>-0.36, -0.22</td>
<td>-8.29</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Activity</td>
<td>0.32</td>
<td>0.03</td>
<td>0.25, 0.38</td>
<td>9.52</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Season</td>
<td>0.08</td>
<td>0.03</td>
<td>0.02, 0.15</td>
<td>2.45</td>
<td>0.01</td>
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<tr>
<td></td>
<td>Group</td>
<td>Variance</td>
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<tr>
<td></td>
<td>Residual</td>
<td>Variance</td>
<td>0.17</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Bold indicates factors significant at $P < 0.05$, with values obtained using likelihood-ratio test.

$\beta$ standardised regression coefficient, SE standard error, CI confidence interval, t t-value

Exotic species in Mandena

There were five plant species in Mandena classified as exotics, likely the consequence of human activities and then dispersed in various ways (e.g., wind). These were broad-leaved paperbark tree (*Melaleuca quinquenervia*), guava (*Psidium* spp.), Pemba grass (*Stenotaphrum dimidiatum*), Polynesian arrowroot (*Tacca leontopetaloides*) and soapbush (*Clidemia hirta*). We
observed *H. meridionalis* feeding on *M. quinquenervia* flowers and resting in this species, while they fed on the leaves (grass blades) of *S. dimidiatum*. We observed *E. collaris* using four exotic species, feeding on the ripe fruits of *C. hirta*, *Psidium* spp., and *T. leontopetaloides*, and resting in *M. quinquenervia*. *H. meridionalis* used exotics in 33 of 36 total months (6.6 ± 1.5% of plants used monthly), whereas *E. collaris* only used exotic plant species in four of 19 total months (0.3 ± 0.2% of plants used monthly). The model with the best predictive value (AIC = 105.91, $\chi^2 = 1.33$, df = 1, $P < 0.001$) showed that exotic plants were most likely to be used by *H. meridionalis*, and most often for feeding (Table 4). Season was not included in the best-fit model.

**Table 4.** Generalized linear mixed model predicting monthly utilisation of exotic plants. Data were collected between March 2011 and January 2012 on *E. collaris*, and between January and December 2013 on *H. meridionalis*.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$B$</th>
<th>SE</th>
<th>95% CI</th>
<th>Z</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fixed effects</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-1.52</td>
<td>0.74</td>
<td>-3.24, 0.07</td>
<td>-2.07</td>
<td></td>
</tr>
<tr>
<td>Lemur species</td>
<td>3.39</td>
<td>0.94</td>
<td>1.47, 5.68</td>
<td>3.63</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Activity</td>
<td>-2.45</td>
<td>0.61</td>
<td>-3.78, -1.35</td>
<td>-4.05</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Random effect</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Bold indicates factors significant at $P < 0.05$.

$SE$ standard error, $CI$ confidence interval

**Discussion**

Similar to Lehman et al. (2006), we found that both *E. collaris* and *H. meridionalis* used similar proportions of forest edge habitat within their home ranges and core areas, thus our prediction that *H. meridionalis* would use greater edge habitat was not supported. As predicted, the frugivorous *E. collaris* was more likely to use both slow- and mid-growing plant species, while the folivorous *H. meridionalis* was more likely to use fast-growing plants in Mandena. In terms of activity, slow-growing trees were particularly important for *E. collaris* resting, in line
with our prediction, while *H. meridionalis* used a similarly large amount of slow-growing trees
for resting. As expected, fast-growing plants (comprising mostly herbs and scrubs) seem to be
preferred by *H. meridionalis* which exhibited greater ability to include pioneer species in its diet,
a finding that is consistent with other studies of folivorous primates (Bicca-Marques and
Calegaro-Marques 1994; Bonilla-Sánchez et al. 2012; Ganzhorn et al. 1999b). However, the use
of exotic (non-endemic) plant species for feeding by *H. meridionalis* did not support our
prediction, as these small-bodied folivores consumed items from these non-native plants nearly
every month.

Although bamboo lemurs are folivores, they are often considered to be dietary specialists
due to the large proportion of their feeding focused on bamboos (Ballhorn et al. 2016; Tan 1999).
However, when there are alternative habitats adjacent to a degraded habitat (e.g., mangrove
swamp, mono-dominant plantation), even dietary specialists can adapt and exploit them (Galat-
Luong and Galat 2005; Grimes and Paterson 2000; Nowak 2008). Such is the case with bamboo
lemurs which have been observed to use alternative and/or degraded habitats (Grassi 2006;
Martinez 2008; Wright et al. 2008; Eppley et al. 2015a). Furthermore, the occasional use of
wetland habitat by primates may become obligate if preferred upland habitat becomes
increasingly disturbed (Nowak 2008, 2013; Quinten et al. 2010); however, when species are
highly selective within their habitat, the loss of key resources may result in their ultimate demise
(Lee and Hauser 1998). In contrast, low selectivity may enhance a species’ chances for survival,
even in heavily disturbed habitats (Guo et al. 2008).

In general, bamboo lemurs (*Hapalemur* spp. / *Prolemur simus*) appear less susceptible to
habitat degradation than more frugivorous species, i.e., *Propithecus* spp., *Eulemur* spp., *Varecia*
spp. (Arrigo-Nelson 2006; Dehgan 2003; Irwin et al. 2010; Schwitzer et al. 2007). Despite this,
there appears to be some variation in bamboo lemur responses to degraded habitats. For example, *H. occidentalis* have been observed to feed on invasive *C. hirta* and crop forage on rice (*Oryza sativa*) in agricultural fields adjacent to Masoala National Park (Martinez 2008), while *H. griseus* have been observed shift their diet to exotic guava (*P. cattleianum*) during fruiting periods in a previously selectively logged area of Ranomafana National Park (Grassi 2006). Furthermore, the greater bamboo lemur (*P. simus*) is known to inhabit shaded coffee plantations (Wright et al. 2008). Similar to these fragment-tolerant bamboo lemurs, *H. meridionalis* displayed an ability to adjust across various habitats (i.e., littoral forest, littoral swamp, and an invasive Melaleuca-dominated swamp), and though this was slightly seasonal, they were able to feed and rest for large portions of time in each habitat in all seasons (Eppley et al. 2015a). Additionally, they exhibited the highest dietary diversity recorded for a bamboo lemur species (Eppley et al. 2016a). In addition to the flexible activity pattern exhibited by *H. meridionalis* in Mandena, these lemurs are also able to adjust flexibly to contrasting floristic and structural habitats, exploiting resources that are specific to each environment (Eppley et al. 2015a, 2016a).

Two previous studies on *E. collaris* in Mandena indicate that these lemurs in the fragmented littoral forest tend to remain highly frugivorous but they expand their home range when compared to less disturbed forests (Campera et al. 2014; Donati et al. 2011). This flexible strategy differs from other brown lemur populations that seem to be able to shift seasonally to a more folivorous diet (e.g., *E. macaco macaco*; Colquhoun 1997, *E. mongoz*; Curtis 2004, *E. rufifrons*; Sussman 1977), and for a detailed meta-analysis, see Sato et al. (2016). The feeding preference of *E. collaris* for mid- and slow-growing species, that tend to represent large trees rather than herbs/scrubs and thus are rarer in highly fragmented areas than in pristine forest, is in line with an expansion of the threshold of area requirement. Our results show a preference of *E.*
collaris for mid-growing species in the dry seasons while slow-growing, usually climax trees, are selected more often in the wet season. This is an indication that E. collaris may tend to use pioneer species more frequently during periods of low resource abundance (e.g., the dry season in Mandena) when climax trees show phenological bottlenecks. This hypothesis is worth exploring in future studies matching fine-grained phenological data with lemur seasonal feeding.

The preference for fruiting trees does not mean that E. collaris is not capable of using pioneer or exotic species growing in edge areas both for feeding and for resting, as indicated by the similar values of edge use and their use of four exotic plant species. In Mandena, E. collaris have been seen to move in the periphery of forest fragments in order to feed on fruits of the exotic Psidium spp. (Campera et al. 2014; Donati et al. 2011) and domestic lychee (Litchi chinensis; Donati pers. observ.). In Ste. Luce (20 km north of Mandena), E. collaris have also been observed to move to the forest edge, or even outside of it, to feed on the fruits of exotic and/or pioneer species, e.g., the fruits of the pioneer meramaintso (Sarcolaena multiflora; Campera et al. 2014). This pattern does not seem to be unusual for brown lemurs even in less disturbed forests as migrations from familiar areas to feed on exotic Psidium spp. have also been recorded in E. rufifrons in Ranomafana (Overdorff 1993; Wright 1999).

In areas more heavily affected by habitat alteration, the genus Eulemur may rely heavily on exotic trees, in most cases for fruits or for resting/sleeping. In the gallery forest fragment of Berenty, during specific periods of the year the hybrids E. rufifrons x E. collaris base the majority of their diet on fruits of the exotic Manilla tamarind (Pithecellobium dulce; Donati, unpublished data). In Ampasikely, a 50-ha coastal private landholding located in northwestern Madagascar, E. macaco feed on 23 exotic plant species that were introduced as cash crops, such as coffee (Coffea spp.), papaya (Carica papaya), mango (Mangifera indica), and lebbeck or
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woman’s tongue (*Albizia lebbeck*; Simmen et al. 2007). Thus, the low level of reliance on exotic species by *E. collaris* recorded in our study seems to be more the consequence of the low frequency of suitable exotic species than the lack of flexibility of these collared brown lemurs to include unusual food species in their diet.

Habitat disturbance may benefit folivorous lemurs in several ways. It can increase the heterogeneity of a forest and therefore increase the amount or density of food resources (Oates 1996). Disturbance can increase the relative abundance of certain plant species that may be preferred food sources, such as pioneer and light-gap species, and terrestrial herbaceous vegetation (Oates 1996). Light gaps created by tree falls and/or selective felling may help to maintain floristic diversity by harbouring a higher density of tree stems (Brokaw and Busing 2000). These gaps can also increase the number of early successional specialists, which tend to have leaves with increased protein, less fibre, and lower phenolic content, as well as increasing the quantity of young leaves and improving the quality of mature leaves (Chapman et al. 2002; Ganzhorn 1992, 1995; Oates, 1996). Our finding that *H. meridionalis* exhibit a flexible behavioural and feeding ecology is not all that surprising. Bamboo lemur congeners exploit bamboo, which is highly prevalent in their habitat and thrives particularly well in slightly disturbed areas. The increased sunlight reaching both the canopy and forest floor further increases the quantity and quality of staple foods (bamboo and leaves) and provides higher quality supplemental foods (light-gap species and introduced species). Furthermore, similar to our *H. meridionalis* results, *H. griseus* in Ranomafana National Park exhibit a tolerance to forest edge (Lehman et al. 2006). Ultimately, the ability to use forest edge may have future benefits, in that altered landscapes with habitat matrices could provide potential conservation value as vital refuges (Chapman and Lambert 2000; Riley 2007).
Various folivorous primates, i.e., *Alouatta* spp., are able to inhabit anthropogenically-disturbed habitats, likely due to a broad range of behavioural adaptations (Bonilla-Sánchez et al. 2012; Zárate et al. 2014). Notably, within these habitats howler monkeys are able to flexibly increase their dietary breadth (Bicca-Marques 2003), similar to observations of *H. meridionalis* in Mandena (Eppley et al. 2016a). By comparison, arboreal frugivores such as brown spider monkeys (*Ateles hybridus*) are not as flexible, and have been shown to be adversely affected by the constraints of living in an anthropogenic, degraded forest (Marsh et al. 2016). This is not always the case, however, as even frugivorous primates, e.g., red-bellied lemurs (*E. rubriventer*), display an ability to utilise and be tolerant of forest edge (Lehman et al. 2006). Although *E. collaris* and *H. meridionalis* displayed differences in the degree of pioneer exotic plant species they used, the both used similar proportions of forest edge within their home ranges and core areas.

The further fragmentation of remaining forests is of great concern if forest species of Madagascar are to persist (Ganzhorn et al. 2014). Although the fate of all lemur species should be considered precarious due to increasing habitat destruction, the knowledge that some lemurs are able to cope with this degradation (to a certain degree) should be seen as positive. Some primate species adapted to narrow ecological specializations may be sensitive to natural or anthropogenic habitat perturbations (Harcourt et al. 2005; Kamilar and Paciulli 2008), whereas others have been shown to adjust to changing environments (Anderson et al. 2007; Nowak and Lee 2013). Not surprisingly, our study on two lemurids living in the highly disturbed littoral forest fragments shows that the lemurs are able to use both pioneer and exotic species for feeding and resting. However, while frugivorous *E. collaris* appear more limited by climax plants,
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folivorous *H. meridionalis* show a wider range of adaptability, probably favoured by its diet and smaller body size.

References


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