

1 **Ecological flexibility as measured by the use of pioneer and exotic plants in two lemurids:**
2 *Eulemur collaris* and *Hapalemur meridionalis*

3

4 **Short title:** Do lemurid diets shape ecological flexibilities?

5

6 **Keywords:** pioneer species; exotic plants; edge habitat; collared brown lemur; southern bamboo
7 lemur; Madagascar

8

9 **Abstract**

10 Primate responses to habitat alteration vary depending on the species' dietary guild and
11 forest type. Leaves from secondary vegetation can provide nutritious resources to folivorous
12 primates, whereas frugivores, burdened with a scattered spatial and temporal distribution of
13 fruiting resources, require larger home ranges, potentially limiting their ability to cope with
14 altered landscapes. Within coastal south-eastern Madagascar, we sought to determine whether
15 two lemur species occupying contrasting ecological niches (i.e., dietary guilds) respond
16 differently to the changing features of their degraded and fragmented habitat. We conducted
17 behavioural observations between 2011 and 2013 on frugivorous collared brown lemurs
18 (*Eulemur collaris*) and folivorous southern bamboo lemurs (*Hapalemur meridionalis*). In order
19 to estimate the ability of lemurs to use pioneer species, we categorised all plants used for feeding
20 and resting as either 'fast-growing', 'mid-growing', or 'slow-growing'. We fitted linear mixed-
21 effects models, one for each plant growth category with monthly proportional use rates as the
22 dependent variable, and included species (*E. collaris* and *H. meridionalis*), activity (feeding and
23 resting), and season (dry and wet) as fixed effects. Our results show that *E. collaris* used both

24 slow- and mid-growing plant species most often, while *H. meridionalis* were more likely to use
25 fast-growing plants, which indicated an ability to utilise secondary/disturbed vegetation.
26 Frugivorous *E. collaris* appear more limited by climax plants, while folivorous *H. meridionalis*
27 appear to be slightly more adaptable, a finding that is consistent with other primate folivores.

28

29 **Introduction**

30 Tropical deforestation is one of the primary threats to global biodiversity (Achard et al.
31 2002; Asner et al. 2009; Dirzo and Raven 2003; Gibson et al. 2011; Sala et al. 2000). The
32 destruction, fragmentation, and degradation of remaining habitats threaten many species' ability
33 to survive (Oates 2013). While forest fragments typically persist after deforestation, they
34 effectively become islands within an anthropogenic landscape, most of which are unsuitable
35 habitat for the majority of forest species (Broadbent et al. 2008; Laurance et al. 2009, 2011).

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

43 It is important to understand behavioural responses of forest dwelling primates to habitat
44 degradation and fragmentation due to the increasing rate of habitat alteration and limited ability
45 of most species to move between forest fragments (Marsh 2003). How a primate responds to
46 habitat degradation, however, seems to vary depending on species and type of forest (Chapman

47 et al. 2000; Cowlshaw and Dunbar 2000; Onderdonk and Chapman 2000). Secondary growth
48 may produce foods of higher dietary quality compared to foods available in mature forests, thus
49 making folivorous (i.e., leaf-eating) primates less affected by habitat degradation (Chapman et al.
50 2002; Ganzhorn 1995; Ganzhorn et al. 1999b; Plumptre and Reynolds 1994). For example,
51 populations of folivorous black howler monkeys (*Alouatta caraya* and *A. pigra*), have been
52 documented to use and rely heavily on fast-growing, exotic plant species (e.g., *Eucalyptus* and
53 shaded cocoa plantations) for both occasional food and resting/sleeping within fragmented,
54 anthropogenic landscapes (Bicca-Marques and Calegario-Marques 1994; Bonilla-Sánchez et al.
55 2012; Zárate et al. 2014). Similarly, black-and-white colobus (*Colobus guereza*) appear to do
56 well in some disturbed (i.e., previously logged) habitats (Chapman et al. 2000; Tutin et al.
57 1997b). Frugivorous (i.e., fruit-eating) primates, however, have to cope with the scattered spatial
58 and temporal distribution of fruiting resources, thus often requiring larger home ranges (Estrada
59 and Coates-Estrada 1996; Rode et al. 2006; but see Tutin et al. 1997a). Many frugivorous
60 primates avoid forest fragments, e.g., grey-cheeked mangabeys (*Lophocebus albigena*) and
61 Mexican spider monkeys (*Ateles geoffroyi vellerosus*), and appear to be restricted to continuous
62 forests (Estrada and Coates-Estrada 1996; Tutin et al. 1997b). Despite these potential limitations,
63 some frugivorous primates, such as chimpanzees (*Pan troglodytes*) and Sumatran orangutans
64 (*Pongo abelii*), demonstrate an ability to survive within degraded, anthropogenic landscapes,
65 foraging on a mixture of crops and wild fruits (Campbell-Smith et al. 2011; Hockings and
66 McLennan 2012; McLennan and Hockings 2014). As frugivorous primates are important seed
67 dispersers, their ability to cope within anthropogenic landscapes has major implications for the
68 maintenance of forest diversity: they are fundamental in the regeneration of degraded habitats
69 (Chapman 1995; Ganzhorn 1995; Razafindratsima and Dunham 2014).

70 On a global scale, frugivorous strepsirrhines from Madagascar contribute on a larger
71 scale to their respective ecosystems, e.g., seed dispersal, compared to primates in the Neotropics
72 or mainland Africa (Jernvall and Wright 1998). As frugivorous lemurs are essential to
73 maintaining the unique forests of Madagascar, their demise would likely trigger extinction
74 cascades (Federman et al. 2016; Ganzhorn et al. 1999a; Jernvall and Wright 1998;
75 Razafindratsima and Dunham 2014). Within Madagascar, for example, greater than 80% of
76 forest area exists less than 1 kilometre from an edge (Harper et al. 2007), and thus fragmentation
77 is of great concern for the survival of forest fauna and flora species (Hannah et al. 2008; Waeber
78 et al. 2015). This can be further complicated by introduced exotic and invasive species that
79 threaten the preservation of endemic biodiversity as well as ecosystem restoration efforts
80 (Braithwaite et al. 1989; D'Antonio and Vitousek 1992). While the limits of lemurs' tolerance,
81 i.e., coping strategies, to fragmented, secondary, and degraded habitats are poorly understood
82 (Campera et al. 2014; Donati et al. 2011; Eppley et al. 2015a; Gardner 2009; Irwin et al. 2010;
83 Lehman et al. 2006), it is imperative to understand the relationship between species and these
84 altered habitats if we are to properly conserve primates and other species (Cristóbal-Azkarate
85 and Arroyo-Rodríguez 2007; Isabirye-Basuta and Lwanga 2008; Onderdonk and Chapman
86 2000).

87 The Anosy region along the southeast coast of Madagascar provides a complex mosaic of
88 heavily fragmented upland and swamp forest habitats, mono-dominant exotic species, old and
89 new timber plantations, and a large-scale ilmenite ore mine and separation plant facility
90 (Barthlott et al. 1996; Ramanamanjato et al. 2002; Ganzhorn et al. 2007b). This area provides an
91 excellent model with which to explore the behavioural and feeding ecological flexibilities
92 amongst the lemurs which inhabit it (Bollen and Donati 2006; Eppley et al. 2015a;

93 Rabenantoandro et al. 2007), and how they cope with habitat disturbance. Within southeast
94 Madagascar, sympatric collared brown lemur (*Eulemur collaris*) and southern bamboo lemur
95 (*Hapalemur meridionalis*) occupy different ecological niches, the frugivorous and folivorous
96 dietary guild, respectively. Previous research has shown that *E. collaris* is tolerant to habitat
97 degradation and strong seasonal resource availability by flexibly modifying many aspects of its
98 behavioural ecology, such as feeding strategies and home range use (Campera et al. 2014; Donati
99 et al. 2011). Similarly, *H. meridionalis* display a flexible ecology, utilising three distinct habitats
100 (littoral forest, littoral swamp, and *Melaleuca*-dominated swamp) for both resting and feeding
101 purposes (Eppley et al. 2015a).

102 While the use of disturbed habitats by these two lemurids has been increasingly
103 documented (Campera et al. 2014; Eppley et al. 2015a), our study sought to contrast the two taxa
104 and specifically determine to what extent their ecological flexibility played a role in their ability
105 to use altered and degraded habitats. Habitat edges often contain a higher abundance of pioneer,
106 i.e., fast-growing, species as compared to climax habitat (Laurance et al. 2006, 2007).
107 Furthermore, climax, i.e., slow-growing, plants struggle to regenerate in open habitats as is very
108 often the case in edge areas and/or plantations (Benitez-Malvido 1998). The general observation
109 that folivores are able to cope better within degraded environments led us to predict that *H.*
110 *meridionalis* will use more forest edge habitat compared to *E. collaris*. In terms of utilising plant
111 species as feeding and/or resting resources, we sought to determine whether the dietary guilds of
112 our two taxa are predictive of an ability to use fast growing plant species, typically represented
113 by pioneer species, and how this is a potential signal of ecological flexibility to altered habitats.
114 As fast-growing tropical plant species often provide a continuous (i.e., non-seasonal) and
115 relatively large biomass presence of young leaves (Coley et al. 1985; Poorter 1999), which

116 consequently produce more protein (Wasserman and Chapman 2003), we predict that *H.*
117 *meridionalis* will use fast-growing tree species more often than sympatric frugivorous *E.*
118 *collaris*. Due to the contrasting dietary guilds of our two study species, we predict that there will
119 be little overlap in feeding resources. As these are the two largest lemur species within the
120 southeast coastal landscape, however, we predict that they will use similar tree species for
121 resting, as this degraded littoral environment has a limited number of mature trees. We expect
122 the largest differences in feeding tree use to be evident for *E. collaris* during the dry season, i.e.,
123 when there are fewer available food resources (Bollen and Donati 2005; Campera et al. 2014).
124 Lastly, exotic plant species (e.g., introduced, non-endemic), are shown to incur lower levels of
125 leaf herbivory compared to endemic plant species (Lake and Leishman 2004). Thus, we predict
126 that the folivorous *H. meridionalis* would avoid exotic plant species.

127

128 **Methods**

129 Study site

130 We conducted our study in the Mandena Conservation Zone (24°95'S 46°99'E; hereafter
131 Mandena), along the southeast coast of Madagascar, approximately 10 km north of Fort-Dauphin
132 (Tolagnaro). Located within three kilometres of the coast and characterized by a low canopy
133 growing on sandy substrate (Dumetz 1999), this protected area consists of approximately 82 ha
134 of seasonally inundated swamp among 148 ha of degraded littoral forest fragments (Ganzhorn et
135 al. 2007a). This littoral zone experiences less seasonality than the humid eastern forests (Bollen
136 and Donati 2005), with a mean temperature of 22.5°C (range: 9.5 – 35.0°C) and total annual
137 precipitation of 2,808mm, typically generating a wet season between November and April
138 (Eppley et al. 2015a, 2016b). Compared to the less degraded littoral forests further north (Bollen

139 and Donati, 2006), the degree of anthropogenic degradation in Mandena resulted from the
140 historical extraction of utilitarian timber species and charcoal production due to the close
141 proximity of the Anosy region capital (Ingram and Dawson 2006; Vincelette et al. 2007b). The
142 area immediately surrounding these fragmented forests is composed of mono-dominant timber
143 plantations, an exposed sand-scrub matrix, and the large-scale ilmenite mining concession and
144 associated administration and extraction/separation facilities (Ganzhorn et al. 2007b). In addition
145 to the two cathemeral lemurids, i.e., *E. collaris* and *H. meridionalis*, this littoral area is inhabited
146 by four nocturnal strepsirrhines: Ganzhorn's mouse lemur (*Microcebus ganzhorni*), eastern fat-
147 tailed dwarf lemur (*Cheirogaleus medius*), greater dwarf lemur (*C. major*), and the southern
148 woolly lemur (*Avahi meridionalis*).

149

150 Study species

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

160 We captured lemur subjects via Telinject® blow darts (administered by an experienced
161 Malagasy technician) containing a hypnotic anaesthesia (4-5 mg/kg of ketamine hydrochloride or

162 tiletamine hydrochloride. Four individuals (one for each group) of *E. collaris* were captured and
163 equipped with radio-collars (TW-3, Biotrack, 29 g). We captured ten individuals of *H.*
164 *meridionalis* from four social groups, and radio-collared with data-logging tags (ARC400,
165 Advanced Telemetry Systems, Inc.; Isanti, MN, USA). We utilised radio-collars to expedite the
166 amount of time it took to locate lemur groups each day; however, not all adult focal individuals
167 were radio-collared. All subjects recovered from anaesthesia within 1.5 h and were not moved
168 from the capture area. Furthermore, we followed lemurs until they regained full mobility in trees.
169 There were no injuries as a consequence of the captures. The collars were below the 5%
170 threshold of the subjects' weight. For more specific information on the capturing/collaring
171 processes of *E. collaris*, see Campera et al. (2014), and for *H. meridionalis*, see Eppley et al.
172 (2015c, 2016c).

173

174 Data collection

175 We collected data for each species during different years. For *E. collaris*, MB and MC
176 observed group AB from March 2011 to January 2012, and group C from June 2011 to January
177 2012. Data collection was conducted on a focal individual from 06:00 to 18:00 h. We collected
178 behavioural data in 5 min intervals via instantaneous sampling (Altmann 1974), specifically
179 noting the tree species used for feeding and resting. Furthermore, we recorded the position of the
180 focal *E. collaris* individual in 30 min intervals via a handheld GPS. For *H. meridionalis*, TME
181 conducted full-day focal observations (from sunrise to sunset) with groups 1, 2, and 4 (we used
182 group 3 exclusively for home range data collection) between January and December 2013. We
183 identified all observed plant food items consumed by the focal individual, noting the plant
184 species' scientific name, and recorded feeding duration via continuous sampling (Altmann

185 1974). Furthermore, we recorded all instances ≥ 15 min for continuous resting. Lastly, we
186 recorded *H. meridionalis* focal waypoint locations via GPS in 15 min intervals.

187 JR and FR identified all plant species used for feeding and resting by both lemur species,
188 and we categorized these into three successive growth rates as they occur under natural
189 conditions. As such, *fast-growing* plant species reached maturity < 2 years, *mid-growing* plant
190 species reached maturity between 2 – 5 years, while *slow-growing* species reached maturity in $>$
191 5 years, with categories based on previous botanical assessments (cf. Vincelette et al. 2007a).
192 Furthermore, JR identified exotic plant species (i.e., non-endemic), which we validated with an
193 index of exotic and invasive species in Madagascar (Gérard et al. 2015).

194

195 Ethical Note

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

203

204 Data analyses

205 We entered all ranging data into ArcGIS 10.2 (ESRI) using the Geospatial Modelling
206 Environment (GME) spatial ecology interface (Beyer 2012). Ranging and statistical analyses
207 were conducted using R statistical software version 3.2.3 (R Development Core Team 2015). We

208 determined each group home range with a 95% kernel density estimate, while core areas were
209 determined as a 50% kernel density estimate (Worton 1989). We then created a forest edge
210 polygon buffer 100 m inside the littoral forest boundary which allowed us to calculate the total
211 amount of forest edge and non-edge habitat within each lemur species' home range and core
212 areas within Mandena (Laurance et al. 2007; Lehman et al. 2006).

213 From our behavioural sampling of *E. collaris* and *H. meridionalis*, we calculated monthly
214 proportional utilisation rates for all feeding and resting trees. For each of the three plant species
215 growth categorizations, we fitted General Linear Mixed-effects Models (LMM) using the lmer
216 function of the lme4 package developed for R (Bates et al. 2012). For each LMM, our dependent
217 response variable was the monthly proportion of plant species used (i.e., fast-growing plants,
218 mid-growing plants, and slow-growing plants), while our fixed effects were the lemur species (*E.*
219 *collaris* and *H. meridionalis*), activity (feeding and resting), and season (dry and wet). We
220 included lemur social group as random effect to control for repeated sampling. We then used the
221 ANOVA function to calculate likelihood ratio tests for model comparison, allowing us to
222 determine which model had the best explanatory power by comparing Akaike's Information
223 Criterion (AIC) values for all possible models. *P*-values were obtained with a likelihood ratio
224 test using the afex package (Singmann 2014) developed for R, with significance considered at *P*
225 < 0.05. Residuals from the analyses did not deviate from normality according to the
226 Kolmogorov-Smirnov test.

227 To determine which factors are linked to the utilisation of exotic plants within Mandena,
228 we fitted Generalized Linear Mixed-effects Models (GLMM) using the glmer function of the
229 lme4 package developed for R (Bates et al. 2012), with the monthly use of an exotic plant as a
230 binomial dependent variable, as opposed to endemic plants. As with the LMMs, our fixed effects

231 were lemur species, activity, and season, with group included as random effect to control for
232 repeated sampling. We then used the ANOVA function to calculate likelihood ratio tests for
233 model comparison and determined which model had the most explanatory power by comparing
234 the AIC values for all possible models.

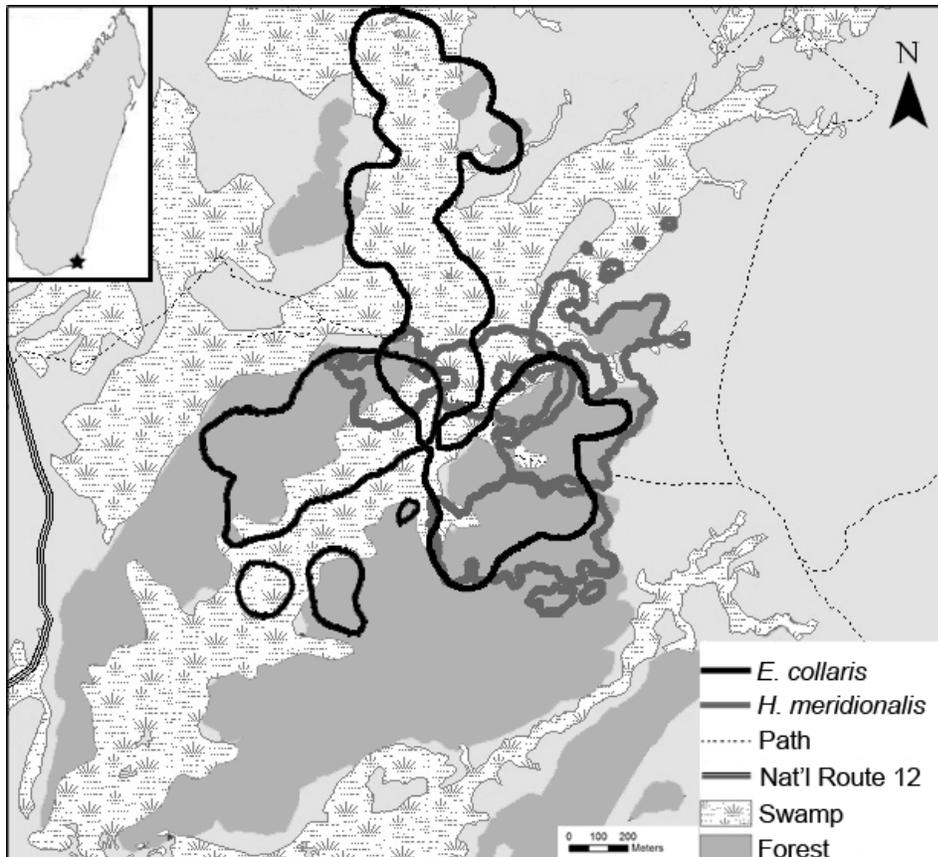
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236 **Results**

237 Ranging

238 We observed *E. collaris* for 962 h, while *H. meridionalis* were observed for 1,762 h. Both
239 lemurid species' home ranges were within the central to northern portions of Mandena, and were
240 not limited to only littoral forest areas, but rather encompassed a mixture of both littoral forest
241 and swamp (Fig. 1). Considering species' home ranges, *E. collaris* used considerably larger areas
242 than *H. meridionalis* (Table 1). The proportion of edge habitat used by both species within their
243 home range were similar, with forest edge comprising a mean of 37.4% of *E. collaris* home
244 ranges (N = 2), and 45.6% of *H. meridionalis* home ranges (N = 4) (Table 1). Considering only
245 the core areas, forest edge comprised similar mean percentages of *E. collaris* (50.6%) and *H.*
246 *meridionalis* (42.6%) habitat.

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249 **Fig. 1.** Location of *E. collaris* and *H. meridionalis* group home ranges (95% kernel density
 250 estimates) within the Mandena littoral forest and swamp. Portions of the swamp are composed of
 251 mono-dominant strands of exotic *Melaleuca*, while lighter grey areas to the east are a sand-scrub
 252 matrix and those to the west are a matrix of sand-scrub and Eucalyptus plantations. Data on *E.*
 253 *collaris* were collected between March 2011 and January 2012, and *H. meridionalis* between
 254 January and December 2013.

255

256 **Table 1.** Area (in hectares) of both home range (95% kernel density estimate) and core area
 257 (50% kernel density estimate) for *E. collaris* and *H. meridionalis* groups in Mandena. Edge
 258 habitat was calculated as the area (ha) within 100 m buffer from the forest edge. Data were
 259 collected on *E. collaris* between March 2011 and January 2012, and on *H. meridionalis* between
 260 January and December 2013.

Species	Group	Months of observation	Home range (ha)			Core area (ha)		
			Edge (ha)	Edge (%)	Edge (ha)	Edge (%)		
<i>E. collaris</i>	AB	11	41.16	19.07	46.33	5.61	4.31	76.83
	C	8	83.32	23.68	28.42	17.98	4.39	24.42
<i>H. meridionalis</i>	1	12	18.39	8.40	45.68	7.76	1.20	15.46
	2	12	17.66	9.75	55.21	3.74	2.68	71.66
	3	12	6.60	3.65	55.30	N/A	N/A	N/A
	4	12	10.43	2.75	26.37	2.09	0.85	40.67

261

262 Diet

263 We identified 105 different plant species used by *E. collaris* and 112 species used by *H.*
 264 *meridionalis* for feeding and resting (Table 2). Twenty-four plant species were eaten by both
 265 lemurs. More specifically, *E. collaris* food resources comprised 16.9% fast-growing, 28.6% mid-
 266 growing, and 54.6% slow-growing plants. For *H. meridionalis*, food resources comprised 38.0%
 267 fast-growing, 16.9% mid-growing, and 45.1% slow-growing plants. Twenty-seven plant species
 268 were used for resting by both lemur species. For *E. collaris*, we categorized 14.3% of all resting
 269 plants as fast-growing, 24.8% as mid-growing, and 61.0% as slow-growing, while for *H.*
 270 *meridionalis*, we categorized 27.7% of their used plants as fast-growing, 14.3% as mid-growing,
 271 and 58.0% as slow-growing. Both *E. collaris* and *H. meridionalis* displayed large differences in
 272 their utilisation of these plant growth categories between activity (Fig. 2) and season (Fig. 3).

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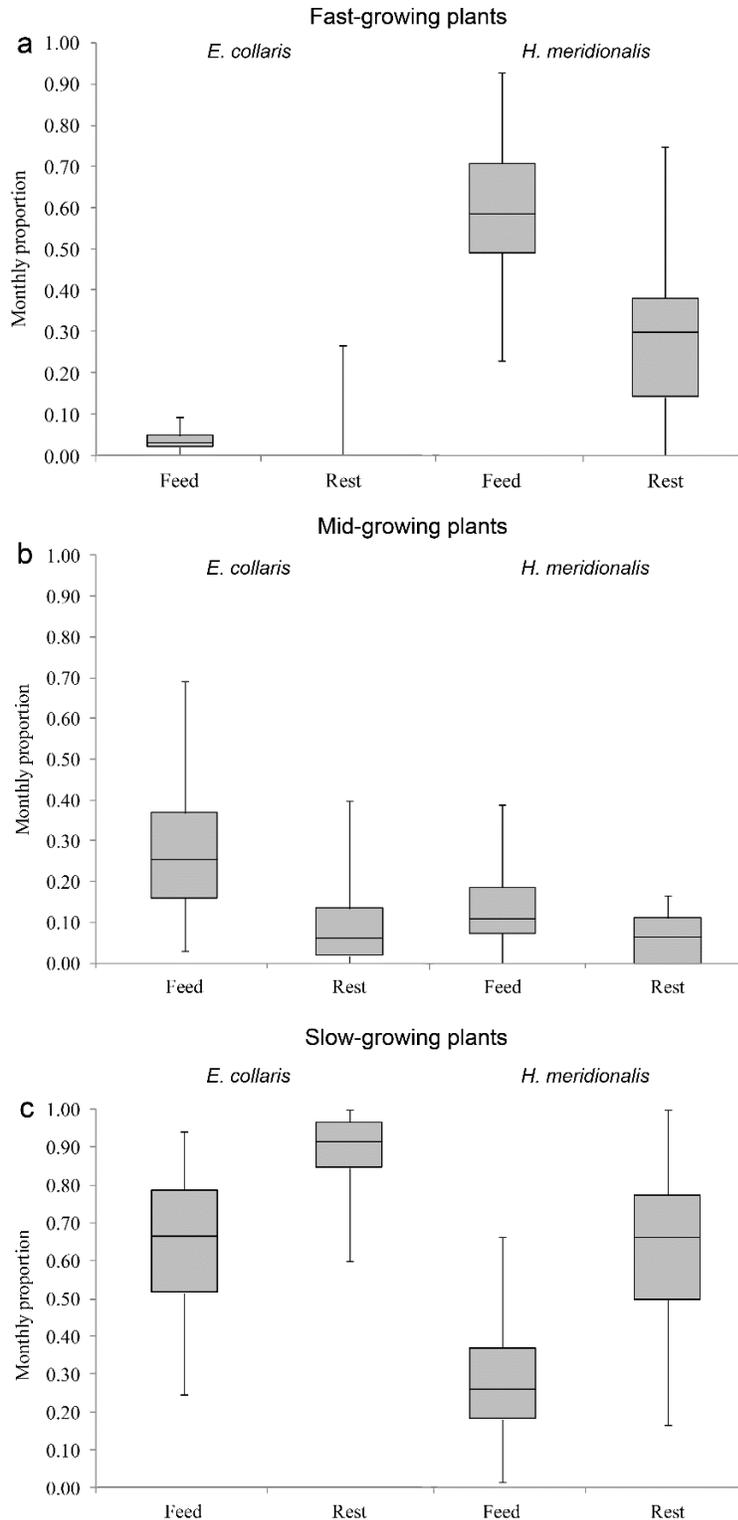
274 **Table 2.** Number of species within feeding and resting plant species' growth categorization for
 275 *E. collaris* (March 2011 to January 2012) and *H. meridionalis* (January to December 2013) in
 276 Mandena.

Plant categories	<i>E. collaris</i>			<i>H. meridionalis</i>		
	Feed	Rest	Total	Feed	Rest	Total
Fast-growing	13	2	15	27	5	31
Mid-growing	22	11	26	12	8	16
Slow-growing	42	43	64	33	57	65

277 Note: *E. collaris* also relied on six unidentified plant species that were not included in the
 278 analyses

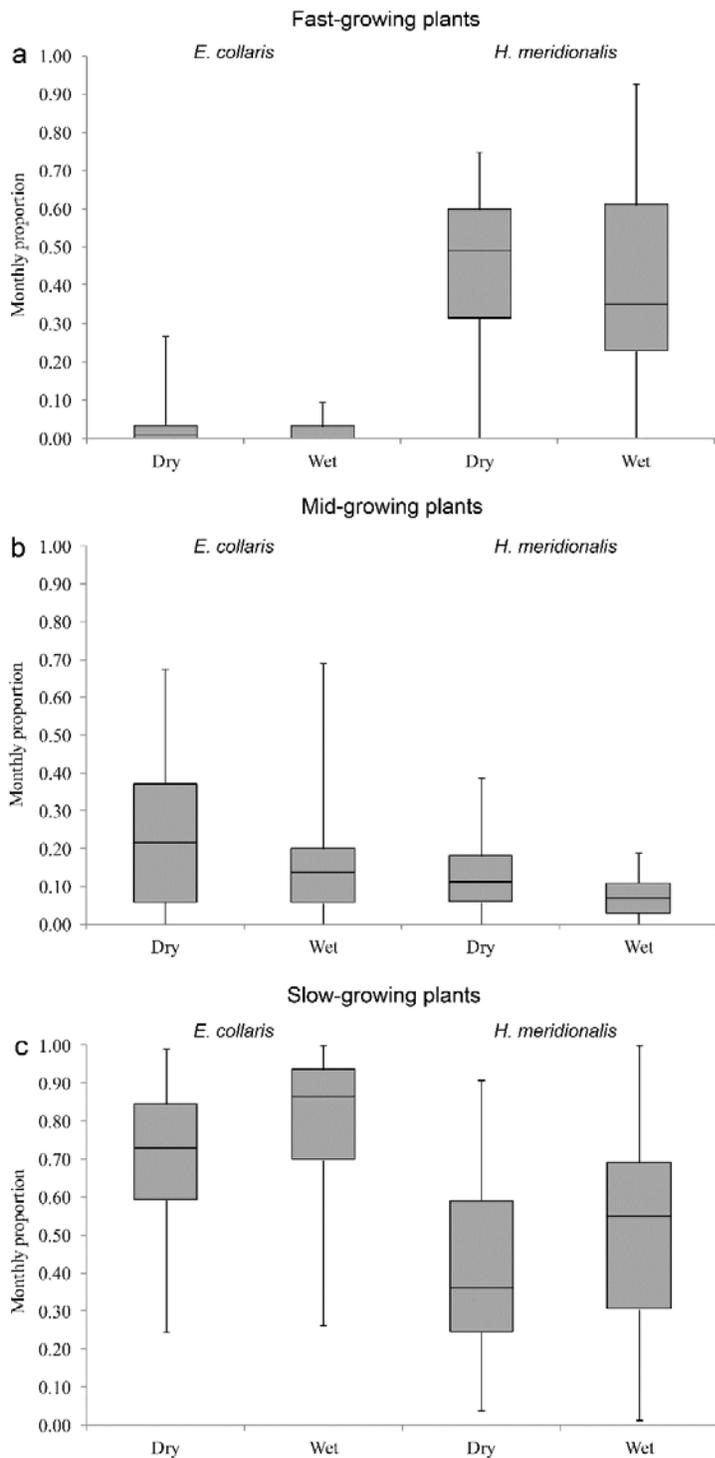
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 282 **Fig. 2.** Comparison of monthly proportional medians (including interquartiles and ranges)
 283 between *E. collaris* and *H. meridionalis* on their selection of (a) fast-growing, (b) mid-growing,
 284 and (c) slow-growing plants for feeding and resting. Data were collected between March 2011
 285 and January 2012 on *E. collaris*, and between January and December 2013 on *H. meridionalis*.

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288 **Fig. 3.** Comparison of monthly proportional medians (including interquartiles and ranges)
 289 between *E. collaris* and *H. meridionalis* on their selection of (a) fast-growing, (b) mid-growing,
 290 and (c) slow-growing plants during the dry and wet seasons. Data were collected between March
 291 2011 and January 2012 on *E. collaris*, and between January and December 2013 on *H.*
 292 *meridionalis*.

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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).

323 **Table 3.** Linear mixed models predicting increased monthly proportion of using fast-growing
 324 plants, mid-growing plants, and slow-growing plants by *E. collaris* and *H. meridionalis* in
 325 Mandena, Madagascar. Data were collected between March 2011 and January 2012 on *E.*
 326 *collaris*, and between January and December 2013 on *H. meridionalis*.

Growth class	Variable	β	SE	95% CI	<i>t</i>	<i>P</i>
<u>Fast-growing</u>						
	<u>Fixed effects</u>					
	Intercept	0.13	0.04	0.06, 0.21	3.42	
	Species	0.41	0.42	0.33, 0.49	9.78	<0.0001
	Activity	-0.19	0.29	-0.25, -0.14	-6.66	<0.0001
	Season	-0.02	0.03	-0.08, 0.03	-0.85	0.39
	<u>Random effect</u>					
	Group	Variance	0.03			
	Residual	Variance	0.15			
<u>Mid-growing</u>						
	<u>Fixed effects</u>					
	Intercept	0.29	0.02	0.24, 0.34	12.24	
	Species	-0.10	0.02	-0.15, -0.06	-4.67	<0.001
	Activity	-0.12	0.02	-0.16, -0.08	-5.47	<0.0001
	Season	-0.06	0.02	-0.10, -0.02	-2.74	<0.01
	<u>Random effect</u>					
	Group	Variance	0.00			
	Residual	Variance	0.11			
<u>Slow-growing</u>						
	<u>Fixed effects</u>					
	Intercept	0.55	0.04	0.48, 0.63	14.86	
	Species	-0.29	0.04	-0.36, -0.22	-8.29	<0.0001
	Activity	0.32	0.03	0.25, 0.38	9.52	<0.0001
	Season	0.08	0.03	0.02, 0.15	2.45	0.01
	<u>Random effect</u>					
	Group	Variance	0.00			
	Residual	Variance	0.17			

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

328 β standardised regression coefficient, *SE* standard error, *CI* confidence interval, *t* t-value

329

330 Exotic species in Mandena

331 There were five plant species in Mandena classified as exotics, likely the consequence of

332 human activities and then dispersed in various ways (e.g., wind). These were broad-leaved

333 paperbark tree (*Melaleuca quinquenervia*), guava (*Psidium* spp.), Pemba grass (*Stenotaphrum*

334 *dimidiatum*), Polynesian arrowroot (*Tacca leontopetaloides*) and soapbush (*Clidemia hirta*). We

335 observed *H. meridionalis* feeding on *M. quinquenervia* flowers and resting in this species, while
 336 they fed on the leaves (grass blades) of *S. dimidiatum*. We observed *E. collaris* using four exotic
 337 species, feeding on the ripe fruits of *C. hirta*, *Psidium* spp., and *T. leontopetaloides*, and resting
 338 in *M. quinquenervia*. *H. meridionalis* used exotics in 33 of 36 total months ($6.6 \pm 1.5\%$ of plants
 339 used monthly), whereas *E. collaris* only used exotic plant species in four of 19 total months (0.3
 340 $\pm 0.2\%$ of plants used monthly). The model with the best predictive value ($AIC = 105.91$, $\chi^2 =$
 341 1.33 , $df = 1$, $P < 0.001$) showed that exotic plants were most likely to be used by *H. meridionalis*,
 342 and most often for feeding (Table 4). Season was not included in the best-fit model.

343

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

Variable	<i>B</i>	SE	95% CI	<i>Z</i>	<i>P</i>
<u>Fixed effects</u>					
Intercept	-1.52	0.74	-3.24, 0.07	-2.07	
Lemur species	3.39	0.94	1.47, 5.68	3.63	<0.01
Activity	-2.45	0.61	-3.78, -1.35	-4.05	<0.0001
<u>Random effect</u>					
Group	Variance	0.66			

347 Bold indicates factors significant at $P < 0.05$.

348 *SE* standard error, *CI* confidence interval

349

350 Discussion

351 Similar to Lehman et al. (2006), we found that both *E. collaris* and *H. meridionalis* used
 352 similar proportions of forest edge habitat within their home ranges and core areas, thus our
 353 prediction that *H. meridionalis* would use greater edge habitat was not supported. As predicted,
 354 the frugivorous *E. collaris* was more likely to use both slow- and mid-growing plant species,
 355 while the folivorous *H. meridionalis* was more likely to use fast-growing plants in Mandena. In
 356 terms of activity, slow-growing trees were particularly important for *E. collaris* resting, in line

357 with our prediction, while *H. meridionalis* used a similarly large amount of slow-growing trees
358 for resting. As expected, fast-growing plants (comprising mostly herbs and scrubs) seem to be
359 preferred by *H. meridionalis* which exhibited greater ability to include pioneer species in its diet,
360 a finding that is consistent with other studies of folivorous primates (Bicca-Marques and
361 Calegario-Marques 1994; Bonilla-Sánchez et al. 2012; Ganzhorn et al. 1999b). However, the use
362 of exotic (non-endemic) plant species for feeding by *H. meridionalis* did not support our
363 prediction, as these small-bodied folivores consumed items from these non-native plants nearly
364 every month.

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

377 In general, bamboo lemurs (*Hapalemur* spp. / *Prolemur simus*) appear less susceptible to
378 habitat degradation than more frugivorous species, i.e., *Propithecus* spp., *Eulemur* spp., *Varecia*
379 spp. (Arrigo-Nelson 2006; Dehgan 2003; Irwin et al. 2010; Schwitzer et al. 2007). Despite this,

380 there appears to be some variation in bamboo lemur responses to degraded habitats. For example,
381 *H. occidentalis* have been observed to feed on invasive *C. hirta* and crop forage on rice (*Oryza*
382 *sativa*) in agricultural fields adjacent to Masoala National Park (Martinez 2008), while *H. griseus*
383 have been observed shift their diet to exotic guava (*P. cattleianum*) during fruiting periods in a
384 previously selectively logged area of Ranomafana National Park (Grassi 2006). Furthermore, the
385 greater bamboo lemur (*P. simus*) is known to inhabit shaded coffee plantations (Wright et al.
386 2008). Similar to these fragment-tolerant bamboo lemurs, *H. meridionalis* displayed an ability to
387 adjust across various habitats (i.e., littoral forest, littoral swamp, and an invasive *Melaleuca*-
388 dominated swamp), and though this was slightly seasonal, they were able to feed and rest for
389 large portions of time in each habitat in all seasons (Eppley et al. 2015a). Additionally, they
390 exhibited the highest dietary diversity recorded for a bamboo lemur species (Eppley et al.
391 2016a). In addition to the flexible activity pattern exhibited by *H. meridionalis* in Mandena,
392 these lemurs are also able to adjust flexibly to contrasting floristic and structural habitats,
393 exploiting resources that are specific to each environment (Eppley et al. 2015a, 2016a).

394 Two previous studies on *E. collaris* in Mandena indicate that these lemurs in the
395 fragmented littoral forest tend to remain highly frugivorous but they expand their home range
396 when compared to less disturbed forests (Campera et al. 2014; Donati et al. 2011). This flexible
397 strategy differs from other brown lemur populations that seem to be able to shift seasonally to a
398 more folivorous diet (e.g., *E. macaco macaco*; Colquhoun 1997, *E. mongoz*; Curtis 2004, *E.*
399 *rufifrons*; Sussman 1977), and for a detailed meta-analysis, see Sato et al. (2016). The feeding
400 preference of *E. collaris* for mid- and slow-growing species, that tend to represent large trees
401 rather than herbs/scrubs and thus are rarer in highly fragmented areas than in pristine forest, is in
402 line with an expansion of the threshold of area requirement. Our results show a preference of *E.*

403 *collaris* for mid-growing species in the dry seasons while slow-growing, usually climax trees, are
404 selected more often in the wet season. This is an indication that *E. collaris* may tend to use
405 pioneer species more frequently during periods of low resource abundance (e.g., the dry season
406 in Mandena) when climax trees show phenological bottlenecks. This hypothesis is worth
407 exploring in future studies matching fine-grained phenological data with lemur seasonal feeding.

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

419 In areas more heavily affected by habitat alteration, the genus *Eulemur* may rely heavily
420 on exotic trees, in most cases for fruits or for resting/sleeping. In the gallery forest fragment of
421 Berenty, during specific periods of the year the hybrids *E. rufifrons* x *E. collaris* base the
422 majority of their diet on fruits of the exotic Manilla tamarind (*Pithecellobium dulce*; Donati,
423 unpublished data). In Ampasikely, a 50-ha coastal private landholding located in northwestern
424 Madagascar, *E. macaco* feed on 23 exotic plant species that were introduced as cash crops, such
425 as coffee (*Coffea* spp.), papaya (*Carica papaya*), mango (*Mangifera indica*), and lebeck or

426 woman's tongue (*Albizia lebbbeck*; Simmen et al. 2007). Thus, the low level of reliance on exotic
427 species by *E. collaris* recorded in our study seems to be more the consequence of the low
428 frequency of suitable exotic species than the lack of flexibility of these collared brown lemurs to
429 include unusual food species in their diet.

430 Habitat disturbance may benefit folivorous lemurs in several ways. It can increase the
431 heterogeneity of a forest and therefore increase the amount or density of food resources (Oates
432 1996). Disturbance can increase the relative abundance of certain plant species that may be
433 preferred food sources, such as pioneer and light-gap species, and terrestrial herbaceous
434 vegetation (Oates 1996). Light gaps created by tree falls and/or selective felling may help to
435 maintain floristic diversity by harbouring a higher density of tree stems (Brokaw and Busing
436 2000). These gaps can also increase the number of early successional specialists, which tend to
437 have leaves with increased protein, less fibre, and lower phenolic content, as well as increasing
438 the quantity of young leaves and improving the quality of mature leaves (Chapman et al. 2002;
439 Ganzhorn 1992, 1995; Oates, 1996). Our finding that *H. meridionalis* exhibit a flexible
440 behavioural and feeding ecology is not all that surprising. Bamboo lemur congeners exploit
441 bamboo, which is highly prevalent in their habitat and thrives particularly well in slightly
442 disturbed areas. The increased sunlight reaching both the canopy and forest floor further
443 increases the quantity and quality of staple foods (bamboo and leaves) and provides higher
444 quality supplemental foods (light-gap species and introduced species). Furthermore, similar to
445 our *H. meridionalis* results, *H. griseus* in Ranomafana National Park exhibit a tolerance to forest
446 edge (Lehman et al. 2006). Ultimately, the ability to use forest edge may have future benefits, in
447 that altered landscapes with habitat matrices could provide potential conservation value as vital
448 refuges (Chapman and Lambert 2000; Riley 2007).

449 Various folivorous primates, i.e., *Alouatta* spp., are able to inhabit
450 anthropogenically-disturbed habitats, likely due to a broad range of behavioural adaptations
451 (Bonilla-Sánchez et al. 2012; Zárate et al. 2014). Notably, within these habitats howler
452 monkeys are able to flexibly increase their dietary breadth (Bicca-Marques 2003), similar to
453 observations of *H. meridionalis* in Mandena (Eppley et al. 2016a). By comparison, arboreal
454 frugivores such as brown spider monkeys (*Ateles hybridus*) are not as flexible, and have
455 been shown to be adversely affected by the constraints of living in an anthropogenic,
456 degraded forest (Marsh et al. 2016). This is not always the case, however, as even
457 frugivorous primates, e.g., red-bellied lemurs (*E. rubriventer*), display an ability to utilise
458 and be tolerant of forest edge (Lehman et al. 2006). Although *E. collaris* and *H.*
459 *meridionalis* displayed differences in the degree of pioneer exotic plant species they used,
460 the both used similar proportions of forest edge within their home ranges and core areas.

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

471 folivorous *H. meridionalis* show a wider range of adaptability, probably favoured by its diet and
472 smaller body size.

473

474

475 **References**

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