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running heading: Long-term studies of basal primates

Long-Term Field Studies of Lemurs, Lorises and Tarsiers

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26 Lemurs, lorises, and tarsiers are socially and ecologically diverse primates that
27 include some of the most endangered mammals. We review results of long-term studies
28 of 15 lemur species from 7 sites in Madagascar and 1 species each of loris and tarsier,
29 respectively, in Indonesia. We emphasize that the existence of long-term study
30 populations is a crucial prerequisite for planning and conducting shorter studies on
31 specific topics, as exemplified by various ecophysiological studies of lemurs. Extended
32 studies of known individuals have revealed variation in social organization within and
33 between ecologically similar species. Even in these primates with relatively fast life
34 histories, it required more than a decade of paternity data to characterize male
35 reproductive skew. The long-term consequences of female rank on reproductive success
36 remain poorly known, however. Long-term monitoring of known individuals is the only
37 method to obtain data on life history adaptations, which appear to be shaped by
38 predation in the species covered here; long-term studies are also needed for addressing
39 particular questions in community ecology. The mere presence of long-term projects has
40 a positive effect on the protection of study sites, and they generate unique data that are
41 fundamental to conservation measures, such as close population monitoring.

42

43

Resumen

44 Los lémures, lorises y tarseros son grupos de primates, muy diversos social y
45 ecológicamente, que incluyen algunas de las especies de mamíferos más amenazadas. Se
46 revisaron los resultados de estudios a largo plazo de 15 especies de lémures en 7 áreas
47 de estudio diferentes en Madagascar y una especie de loris y otra de tarsero,
48 respectivamente, en Indonesia. Se resalta la importancia de las áreas de estudio a largo
49 plazo como prerequisite esencial para planear y llevar a cabo asimismo estudios de
50 menor duración sobre temas concretos, como se puede comprobar en varios estudios

51 eco-fisiológicos en lémures, los cuales demuestran interesantes variaciones en estrés y
52 salud entre diferentes hábitats, estaciones y años. Los estudios prolongados sobre
53 individuos conocidos ponen al descubierto importantes variaciones en la organización
54 social tanto dentro de una misma especie como entre especies similares ecológicamente
55 hablando. De la misma manera, estos estudios aportan evidencia de la dispersión de las
56 hembras en algunas especies. Incluso en estos primates, con un ciclo vital relativamente
57 rápido, se necesita recopilar más de una década de datos de paternidad para determinar
58 el sesgo reproductivo de los machos, el cual está especialmente desviado en algunas
59 especies de lémures. Sin embargo, aún se sabe poco de las consecuencias a largo plazo
60 que la posición de las hembras en la jerarquía puede tener en el éxito reproductivo. Se
61 siguen necesitando datos demográficos a largo plazo tanto para supervisar de manera
62 exhaustiva las poblaciones como para abordar cuestiones específicas sobre la ecología
63 de las comunidades. El control a largo plazo de individuos conocidos es además el único
64 método para obtener datos acerca de las adaptaciones históricas que, en el caso de las
65 especies incluidas aquí, parecen haber sido intensamente moldeadas por la depredación.
66 Por último, se discute cómo la existencia de proyectos a largo plazo tiene un efecto
67 protector sobre las áreas de estudio, además de proporcionar datos únicos,
68 fundamentales para la toma de medidas para su conservación.

69

70 Compared to most other mammals, primates are relatively long-lived, endowed with
71 relatively large brains, and characterized by slow life histories (van Schaik and Isler
72 2012), making them important and interesting subjects for comparative long-term field
73 studies (Kappeler et al. 2012). Primates are comprised of 2 infraorders, Strepsirrhini
74 and Haplorrhini; the former includes lemurs and lorises, the latter anthropoids
75 (monkeys and apes) and tarsiers. Formerly, lemurs, lorises, and tarsiers together were

76 referred to as “prosimians,” but it is now clear from molecular studies that they are not 1
77 group. Lemurs and lorises belong to Infraorder Strepsirrhini, and tarsiers (along with
78 anthropoids) belong to Infraorder Haplorrhini (Schmitz et al. 2001). Although
79 Strepsirrhines have some of the faster life histories among living primates, long-term
80 research efforts are still necessary to unravel their diverse social, ecological, and life
81 history adaptations. There are about 100 extant species of lemurs and 30 species of
82 lorises (making up the suborder Strepsirrhini) plus 10 species of tarsiers (Groves 2001).

83 Strepsirrhines and tarsiers have attracted much research interest in recent years
84 because they are socially highly diverse and complex, vary >300 fold in body mass,
85 exhibit diverse ecological adaptations, and, sadly, include some of the most endangered
86 mammals today (Kappeler 2012; Schwitzer et al. 2014). Field research on these
87 primates —lemurs, lorises, and tarsiers — began in the late 1950s and early 1960s
88 (Petter 1962; Charles-Dominique 1970; Jolly 2012), and several of the more recently
89 initiated field projects have turned into long-term studies (>10 years) of 1 or several
90 sympatric species, sometimes by multiple researchers at a given site. Most of these
91 study sites, those for lemurs, are in Madagascar (Fig. 1); they include Berenty (since
92 1963), Beza Mahafaly Special Reserve (since 1975), Ranomafana National Park (since
93 1986), Kirindy (since 1993), Ampijoroa in Ankarafantsika National Park (since 1994),
94 Mandena (since 1997) and Tsinjoarivo (since 2000). Only 1 species of tarsier (*Tarsius*
95 *spectrum*) has been studied for >10 years, and only at Tangkoko Nature Reserve in
96 northern Sulawesi, Indonesia (since 1994). Extended studies of lorises have been
97 confined to *Nycticebus javanaicus* at Cipaganti in West Java, Indonesia (since 2007). We
98 are not aware of any long-term studies of bushbabies (Family Galagidae) or pottos
99 (*Perodicticus potto*). In this paper, we summarize the research highlights emerging from
100 these long-term studies, which involve a total of 17 species (Supplementary data S1;

101 Supplementary data S2). Throughout this review, we emphasize that the existence of
102 long-term study sites is a crucial prerequisite for conducting shorter studies on specific
103 topics covered by the contributions to this special feature.

104 **ECOPHYSIOLOGY**

105 No single ecophysiological study of strepsirrhines and tarsiers has spanned more
106 than a few years, but several important insights into how these primates maintain
107 homeostasis were obtained as a consequence of the establishment of long-term study
108 populations for other reasons. For example, pronounced seasonal variation in climate
109 and food abundance in Madagascar has led to remarkable physiological adaptations
110 among lemurs in Family Cheirogaleidae, which exhibit various patterns of torpor and
111 hibernation that were revealed partly by research at long-term study sites (Schmid and
112 Kappeler 2005; Kobbe et al. 2011; Blanco et al. 2013). Moreover, there seems to be
113 variation in stress physiology between species, sites, and seasons (Pride 2005; Fichtel et
114 al. 2007; Brockman et al. 2009), but studies of longer duration and on other species are
115 required to reveal factors that cause this variation. Short-term studies at several long-
116 term study sites have indicated that health and parasitic infections vary between
117 individuals; it is not clear why they vary, although a number of factors have been
118 implicated. We now need additional studies to disentangle the relative importance of
119 factors such as habitat use (Loudon and Sauther 2013), season (Wright et al. 2009),
120 interannual variation (Clough et al. 2010; King et al. 2012; Radespiel et al. 2015),
121 sociality (Springer et al. 2016), and habitat alteration (Irwin et al. 2010; Singleton et al.
122 2015). We also need these studies to be at more sites, on more species, and for longer
123 duration.

124 **SOCIAL SYSTEMS**

125 The study of social systems can be deconstructed into those focusing on size and
126 composition of social units (social organization) and those focusing on mating patterns
127 and the dynamics of social relationships (i.e., social structure; Kappeler and van Schaik
128 2002). Data collected over years or even decades have contributed substantially to our
129 understanding of the evolution of social systems of strepsirrhines and tarsiers.

130 *Social organization.* — Long-term studies of social organization reveal
131 intraspecific flexibility in some species and striking differences between closely-related,
132 sympatric species. In spectral tarsiers (*Tarsius spectrum*), group size and composition
133 exhibit pronounced intraspecific variation (Gursky 1995), with group composition
134 varying from a single adult male-female pair to groups with multiple adult females and
135 either 1 or multiple adult males and a mean group size of 3.1 individuals (Gursky
136 2010a). In contrast, female gray mouse lemurs (*Microcebus murinus*) at Ankarafantsika
137 form stable matrilineal sleeping groups (Radespiel 2006) in which philopatric females
138 benefit from the presence of mothers or daughters in terms of increased survival
139 (Lutermann et al. 2006); males mostly disperse before the onset of their 1st mating
140 season (Radespiel 2006). Closely-related sympatric Lac Ravelobe mouse lemurs
141 (*Microcebus ravelobensis*), however, form stable mixed-sex sleeping groups consisting of
142 related members of both sexes (Weidt et al. 2004; Radespiel et al. 2009), since young
143 males may delay dispersal and remain in their natal range throughout their 1st mating
144 season. The social organization of *M. murinus* is similar at other sites, where in each case
145 locally sympatric Madame Berthe's mouse lemurs (*Microcebus berthae*) and rufous-gray
146 mouse lemurs (*Microcebus griseorufus*) exhibit yet other patterns of ranging and
147 association (Dammhahn and Kappeler 2009; Génin 2010), suggesting stability in social
148 organization in *M. murinus* across habitats and time.

149 Some of the most important insights into the social organization of strepsirrhines and
150 tarsiers concern natal dispersal patterns. Species differ in their dispersal behavior,
151 which is related to age at 1st reproduction. Hence, a valid understanding of each species
152 requires detailed observation over long periods – up to 5 years in the larger species.

153 In lemurs, male-biased natal dispersal is common in ringtailed lemurs (*Lemur catta*
154 — Sussman 1992; Sauther et al. 1999; Koyama et al. 2001; Parga et al. 2015), Verreaux's
155 sifaka (*Propithecus verreauxi* — Richard et al. 1993; Kappeler and Fichtel 2012a), Milne
156 Edwards's sifaka (*Propithecus edwardsi* — Morelli et al. 2009), and redfronted brown
157 lemurs (*Eulemur rufifrons* — Overdorff et al. 1999; Kappeler and Fichtel 2012b). Long-
158 term genetic and behavioral data have illustrated that, on some occasions, females also
159 emigrate, perhaps due to intense resource competition (*L. catta* — Parga et al. 2015; *E.*
160 *rufifrons* — Kappeler and Fichtel 2012b; *P. verreauxi* — Kappeler and Fichtel 2012a).
161 Female eviction, which can be preceded by targeted aggression, occurs in *L. catta* at
162 Berenty in relatively large groups with many females in the birth or lactation season
163 (Ichino and Koyama 2006), sometimes resulting in troop fission (Koyama 1991; Ichino
164 2006). At Beza Mahafaly, female *L. catta* most often emigrate as mother-daughter
165 groups, and male transfer also occurs, most often among related individuals (Parga et al.
166 2015). Both male and female dispersal have been documented in *P. edwardsi* in
167 Ranomafana National Park, with females transferring between groups on average twice
168 in their lifetimes and males 3 times (Pochron et al. 2004, Morelli et al. 2009).

169 Asian lorises reveal complexity similar to the lemurs. In the Javan slow lorises
170 (*Nycticebus javanicus*), males begin to disperse at 14-18 months of age, slowly making
171 forays from the home range. Female dispersal occurs slightly later and is more directed.
172 Both sexes disperse 1-6 km away from their natal range, and dispersal may occur in
173 stages whereby a young loris attempts to settle, and even pairs for ≤ 1 year with another

174 loris before moving on again (Nekaris 2014). In spectral tarsiers, males disperse twice
175 as far as females do (Gursky 2010b). As a result, only females regularly form territories
176 adjacent to their parental ranges. The site fidelity of individuals that were relocated to
177 their original sleeping tree 5 years later was positively related to the width (diameter at
178 breast height) and height of their sleeping trees. Thus, diverse combinations of social
179 and ecological factors appear to explain dispersal in different species of strepsirrhines
180 and tarsiers, which exhibit deviations from the dominant mammalian pattern of male-
181 only dispersal.

182 *Mating system.* —Long-term studies have informed our understanding of lemur
183 mating systems mainly with respect to male reproductive strategies, which has emerged
184 from genetic paternity data collected over a decade or more. For example, in *P. verreauxi*
185 mating occurs both within and between groups, with great variation in mating
186 competition among the multiple males within a group (Richard 1992; Lawler et al.
187 2005). Paternities also show a mix of within- and extra-group reproduction, and a 10-
188 year study showed that paternity of *P. verreauxi* at Beza Mahafaly is skewed toward a
189 handful of successful males (Lawler 2007). At Kirindy, the dominant male in a sifaka
190 group sired >90% of all infant over more than 10 years, the greatest skew observed in
191 male reproductive success in all primates (Kappeler and Schäffler 2008). Similarly, in *E.*
192 *rufifrons* at Kirindy the most successful males sired on average >70% of all infants over
193 more than 10 years (Kappeler and Port 2008). Male reproductive skew is also
194 pronounced among *M. murinus* at Ankarafantsika where resident males have relatively
195 higher body mass, larger home ranges, and sire relatively more infants than immigrant
196 males (Schmelting et al. 2007). This outcome of intrasexual selection is difficult to
197 reconcile with the lack of sexual dimorphism in lemurs (Kappeler and Fichtel 2015).

198 *Social structure.* — There are fundamental challenges for mammals that live in
199 dispersed social networks. These networks are characterized by individualized stable
200 associations and solitary foraging, and they require coordination of movements,
201 cohesion, and reproduction in time and space, particularly if a species is sympatric with
202 cryptic species of similar body mass. Long-term bioacoustic studies were done on
203 individually marked lemurs of 4 species of the nocturnal lemur community in
204 Ankarafantsika National Park (mouse lemurs, *M. murinus* and *M. ravelobensis*; Milne-
205 Edwards's sportive lemur, *Lepilemur edwardsi*; and the western woolly lemur, *Avahi*
206 *occidentalis*), and it was found that different species exploit different acoustic niches for
207 communication (Zimmermann 2016a). The 2 small-bodied species, the mouse lemurs,
208 use the high frequency (ultrasonic) range as an adaptation to predation. This research
209 also revealed a hitherto neglected role of acoustic signaling in governing group reunion
210 and dispersal as well as species cohesiveness in sympatry, with cues from acoustic
211 structure of the calls that characterize individual identity, sex, kinship, group, or species
212 identity (Zimmermann 2016b). In *L. edwardsi*, pair partners engage in duetting at
213 resource sites, supporting the notion that duetting evolved as a mechanism to
214 coordinate activities between pair partners dispersed in space, to strengthen pair bonds,
215 and to limit infanticide and nutritional stress in lactating females (Méndez-Cárdenas and
216 Zimmermann 2009). Specific syllables within these duets also occur in alarm calls
217 (Scheumann et al. 2007). Acoustic signaling in this nocturnal lemur community allows
218 recognition, even across distance, and consequently gathering of dispersed group
219 members at a particular site and a distinct time; vocal exchanges also help to limit costly,
220 direct intra- and interspecific conflicts (Zimmermann 2016a, 2016b). Furthermore,
221 specific differences in acoustic signaling facilitates the recognition of conspecifics and

222 contribute to cohesiveness of species sympatric with other species (Braune et al. 2008;
223 Zimmermann and Radespiel 2014).

224 Long-term behavioral data also provide important insights into dynamics and
225 function of social relationships, especially with respect to dominance. For example,
226 while overall rates of aggression are relatively low among both *P. verreauxi* and *P.*
227 *edwardsi*, females at Beza Mahafaly are aggressive toward males and consistently elicit
228 submissive signals from them (Kubzdela 1997; Pochron et al. 2003), providing insights
229 into the development of female dominance. As in other taxa, female rank appears to be
230 age-dependent within groups (Kubzdela 1997) and relatively stable over time (Koyama
231 et al. 2005), whereas male-male dominance relationships are more unstable and less
232 age-dependent (Brockman et al. 1998). This is probably because some groups are
233 characterized by large amounts of instability and changes in male membership due to
234 patterns of immigration, emigration, and evictions (Brockman et al. 2001). However,
235 fitness consequences of female rank have only rarely been studied, (Takahata et al.
236 2008), offering an important topic for future analyses of long-term data.

237 **POPULATION AND COMMUNITY ECOLOGY**

238 Long-term monitoring of known individuals is the only method for obtaining
239 information on population dynamics and underlying life history adaptations. Most of the
240 species included in this review have been studied for multiple generations (i.e.,
241 successful reproduction by offspring of individuals known and followed since birth),
242 yielding important comparative data on population dynamics, demography, and life
243 history.

244 *Population dynamics.* — Studies of population density and ranging can yield key
245 information, both for conservation management and for understanding energetic
246 strategies and constraints driving the evolution of social systems. Long-term variation in

247 population abundance and distribution can be the result of species-specific habitat
248 requirements or interspecific competition. Long-term ecological research over a period
249 of more than 15 years at Ankarafantsika suggests that the heterogeneous distribution of
250 *Microcebus* species there is most likely based on species-specific (micro-) habitat
251 preferences related more to divergent patterns of resource use than to interspecific
252 competition (Radespiel 2016). Competitive exclusion may also account for variation in
253 population density in red-bellied lemurs (*Eulemur rubriventer*) and *E. rufifrons*, golden
254 bamboo lemurs (*Hapalemur aureus*) and gray bamboo lemurs (*Hapalemur griseus*), as
255 well as Peyrieras' woolly lemurs (*Avahi peyrierasi*) and the small-toothed sportive lemur
256 (*Lepilemur microdon*) at Ranomafana (Wright et al. 2012).

257 For example, *P. diadema* in more-disturbed habitats at Tsinjoarivo have smaller
258 home range sizes and higher population density, having switched to food resources that
259 are more abundant but lower-quality; they are surviving, but with physiological signs of
260 compromised health (Irwin 2008). Population dynamics of *P. edwardsi* in Ranomafana
261 are also affected by global climate cycles, in that fecundity is compromised by cyclones
262 during gestation (Dunham et al. 2011). In *L. catta* at Berenty, territories were stable
263 over decades but group size is highly variable (Jolly and Pride 1999; Koyama et al. 2006;
264 see Gould et al. 1999). Variation in birth rate, an important driver of group size, was
265 buffered against ecological crises in groups exposed to food-supplementation by tourists
266 (Koyama et al. 2001; Jolly et al. 2002). Population densities of nocturnal lemurs in the
267 same habitat remained stable over 27 years, however (Hladik et al. 1998). Bamboo
268 lemurs in Ranomafana have had 1 or 2 decades of population stability and territory
269 fidelity followed by sudden decreases in numbers of individuals in a group, and even
270 group extinction caused by predation by fossa (*Cryptoprocta ferox*, the largest carnivore
271 on Madagascar) and probably other factors (Wright et al. 2008a, 2014). Thus, long-term

272 monitoring is essential to capture variation in population dynamics over biologically
273 meaningful temporal scales.

274 *Life history.* — There are likely numerous environmental factors that influence
275 the evolution of life history schedules, as there are in other mammals, but so far, the
276 most established connections between environment and lemur life histories pertain to
277 climate (Wright 1999; Dewar and Richard 2007; Dunham et al. 2011). Because
278 strepsirrhines and tarsiers lead relatively slow lives compared to other mammals of the
279 same size, at least 1 decade of continuous monitoring is required, even for the smallest
280 species, which can live to >10 years in the wild (Wright et al. 2008b; Hämäläinen et al.
281 2014; Ichino et al. 2015).

282 Female *P. verreauxi* in the dry deciduous forests at Beza Mahafaly reach sexual
283 maturity around 4 years, but fertility peaks between 7 and 17 years, dropping off after
284 17 years (Richard et al. 2002). This species is long lived (Morris et al. 2011) and is
285 characterized by slow rates of aging (Bronikowski et al. 2011). Relative to their body
286 size, *P. verreauxi* reproduces later and lives longer (up to 19 years) than any other non-
287 human primate species for which there are comparable data (Richard et al. 2002). Many
288 demographic traits such as life expectancy, reproductive value (i.e., an individual's
289 expected future contribution to population growth), and population growth rate exhibits
290 lower values in periods when annual rainfall is low, and a stochastic demographic
291 analysis also shows that population growth rate is depressed as the variance in annual
292 rainfall increases (Lawler et al. 2009). These life history patterns are consistent with
293 theoretical expectation and empirical findings pertaining to life history evolution in an
294 unpredictable climatic environment (Dewar and Richard 2007). Similarly, in high (but
295 still variable) rainfall areas such as Ranomafana, *P. edwardsi* has larger home ranges (50
296 ha) and lower population density, yet the trends of long lifespans (up to 30+ years) and

297 slow development are consistent with data from other species of sifakas, both sympatric
298 species and dry-forest species (Morelli et al. 2009; King et al. 2012; Tecot et al. 2013).

299 Predation is a key source of extrinsic mortality, and local extinction of top predators
300 such as *C. ferox* has created variation in predation rates that also can be compared
301 among study sites. For example, *P. verreauxi* at Kirindy is exposed to higher predation
302 rates than at Beza Mahafaly, where sifakas can live up to 10 years longer (Kappeler and
303 Fichtel 2012a). Irwin et al. (2009) compiled data on *C. ferox* predation of rainforest
304 *Propithecus* from 2 long-term sifaka studies (22 group-years for *P. diadema* at
305 Tsinjoarivo and 73 group-years for *P. edwardsi* at Ranomafana). Although average rates
306 of predation are relatively low (6-7 % of the population taken in a given year), the
307 killings were clustered in time. This suggests that *C. ferox* uses a nomadic hunting
308 strategy, hunting rather intensively in an area before moving on. This type of predation
309 is also a potentially strong force that causes group extinctions, a phenomenon which is
310 especially damaging in the fragmented forests at Tsinjoarivo, where it is unlikely that
311 “empty” forest fragments will be recolonized because of low dispersal rates and the low
312 chance that single individuals will settle.

313 A study of raptor predation at Ranomafana revealed that harrier hawks (*Polyboroides*
314 *radiatus*) and goshawks (*Accipiter henstii*) preyed on 7 species of lemurs, with woolly
315 lemurs and bamboo lemurs the most frequently taken (Karpanty and Wright 2007).
316 Playbacks of raptor calls to *P. edwardsi* individuals elicited alarm calls and male
317 defensive behaviors, suggesting even large-bodied lemurs fear raptor predation
318 (Karpanty 2006). In Ranomafana, predation by ring-tailed mongooses (*Galidia elegans*)
319 on both rufous mouse lemurs (*Microcebus rufus*) and dwarf lemurs (genus *Cheirogaleus*)
320 has been observed, and boas (*Acranthophis dumerili*) eat the smaller lemurs (Wright et
321 al. 2012). Flexibility of life-history traits of small nocturnal lemurs living under different

322 environmental conditions (Lahann et al. 2006) may therefore also be due partly to
323 variation in predation risk.

324 CONSERVATION

325 Long-term field studies have made 2 types of contributions to the conservation of
326 lemurs, lorises, and tarsiers. First, the mere presence of long-term projects, often
327 involving community-based partnerships, has a positive protective effect on the
328 respective study sites, buffering them, at least to some extent, from major local threats
329 (Rabesandratana et al. 2012). In Java the presence of a long-term project has been
330 directly associated with cessation of capture of slow lorises for illegal trade (Nekaris
331 2014). Second, most projects in Madagascar have contributed importantly to
332 understanding human impacts on lemur populations. Many problems face Madagascar's
333 forests — they are highly fragmented, close to villages, become increasingly degraded or
334 completely destroyed, and are subject to rapid climate change (Harper et al. 2007;
335 Hannah et al. 2008). Long-term monitoring of habitat modification and local lemur
336 distributions and abundance provides by far the majority of the data for the re-
337 assessment of conservation status of numerous species (Schwitzer et al. 2014). Direct
338 detrimental effects of anthropogenic activities on lemur health have become especially
339 evident in southern Madagascar (Cuozzo and Sauther 2006; Sauther and Cuozzo 2009;
340 Jolly 2012; Singleton et al. 2015). Negative effects of human-lemur interactions have also
341 been observed in rainforest populations of rufous mouse lemurs occupying forests near
342 villages that are infected with *Giardia* and retroviruses (Zohdy et al. 2015).

343 Long-term presence of researchers is also necessary to assess the feasibility and
344 effectiveness of concrete conservation measures aimed at diminishing the effects of
345 fragmentation, degradation, and possibilities of restoring connectivity between isolated
346 habitats through corridors. Gray mouse lemurs are suitable candidates to address these

347 issues because of their short generation time and high densities. Long-term monitoring
348 reveals that they can use mixed tree plantations, including exotic tree species, as
349 corridors within 5 years after being planted (Andriamandimbiarisoa et al. 2015). Slow
350 lorises, too, have been shown to persist in agricultural plantations if suitable plant
351 species are available (Nekaris 2014). The knowledge that introduced fast growing tree
352 species can be used by lemurs and lorises offers new perspectives for restructuring
353 fragmented landscapes for conservation. Long-term research coupled with conservation
354 genetics can give us important insights into endangered species, providing better
355 assessment of functional genetic diversity in the face of habitat fragmentation (Baden et
356 al. 2014).

357 ADDITIONAL TOPICS

358 Long-term field studies have also contributed to a growing list of food items
359 consumed by lemurs (Simmen et al. 2006) and lorises (Nekaris 2014), as well as records
360 of rare events and behaviors such as vertebrate predation (Ichino and Rambeloarivony
361 2011), predator mobbing (Gursky 2005), cannibalism (Hämäläinen 2012), and
362 infanticide (Erhart and Overdorff 1998; Jolly et al. 2000; Rasoloharijaona et al. 2000;
363 Wright et al. 2012). Moreover, long-term studies have also contributed to understanding
364 the true level of species diversity at several study sites (e.g. Schmid and Kappeler 1994;
365 Zimmermann et al. 1998). Other studies have begun to document patterns of social
366 learning and stable patterns of local behavioral variability across years (Schnoell et al.
367 2014).

368 FUTURE DIRECTIONS

369 Long-term work on several populations of strepsirrhines and tarsiers has now
370 been ongoing for several decades. The biggest challenge for successful continuation of
371 these projects is the implementation of supportive frameworks in terms of political and

372 economic stability in Madagascar and other range countries to allow them to continue.
373 The other side of this coin pertains to the establishment of financial mechanisms for
374 long-term sustainability of field sites in the countries where most of the researchers are
375 currently based. Moreover, to understand fully the evolution and adaptations of these
376 ecologically and socially diverse primate taxa, more long-term field studies are needed,
377 especially on bushbabies (Galagidae; see Kotze et al. 2016) and pottos (*Perodicticus*
378 species). Finally, long-term sites have generated rigorous long-term data, and merging
379 them into a comparative and synthetic data base would now provide the ability to
380 answer a number of big questions in primate biology. The present special feature
381 provides an example of how such integration can be accomplished.

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388

389 SUPPLEMENTARY DATA

390 [Supplementary data S1.](#) - Long-term studies (10 or more years) or those studies with the
391 potential to become long-term studies.

392 [Supplementary data S2.](#) – References cited in S1.

393

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716 **Figure legend**

717 **Fig. 1.** — Location of long-term lemur study sites in Madagascar. Inset shows location of

718 Madagascar off SE coast of Africa.