running heading: Long-term studies of basal primates

Long-Term Field Studies of Lemurs, Lorises and Tarsiers

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

Resumen

Los lémures, lorises y tarseros son grupos de primates, muy diversos social y ecológicamente, que incluyen algunas de las especies de mamíferos más amenazadas. Se revisaron los resultados de estudios a largo plazo de 15 especies de lémures en 7 áreas de estudio diferentes en Madagascar y una especie de loris y otra de tarsero, respectivamente, en Indonesia. Se resalta la importancia de las áreas de estudio a largo plazo como prerrequisito esencial para planear y llevar a cabo asimismo estudios de menor duración sobre temas concretos, como se puede comprobar en varios estudios eco-fisiológicos en lémures, los cuales demuestran interesantes variaciones en estrés y salud entre diferentes hábitats, estaciones y años. Los estudios prolongados sobre individuos conocidos ponen al descubierto importantes variaciones en la organización social tanto dentro de una misma especie como entre especies similares ecológicamente hablando. De la misma manera, estos estudios aportan evidencia de la dispersión de las hembras en algunas especies. Incluso en estos primates, con un ciclo vital relativamente rápido, se necesita recopilar más de una década de datos de paternidad para determinar el sesgo reproductivo de los machos, el cual está especialmente desviado en algunas especies de lémures. Sin embargo, aún se sabe poco de las consecuencias a largo plazo que la posición de las hembras en la jerarquía puede tener en el éxito reproductivo. Se siguen necesitando datos demográficos a largo plazo tanto para supervisar de manera exhaustiva las poblaciones como para abordar cuestiones específicas sobre la ecología de las comunidades. El control a largo plazo de individuos conocidos es además el único método para obtener datos acerca de las adaptaciones históricas que, en el caso de las especies incluidas aquí, parecen haber sido intensamente moldeadas por la depredación. Por último, se discute cómo la existencia de proyectos a largo plazo tiene un efecto protector sobre las áreas de estudio, además de proporcionar datos únicos, fundamentales para la toma de medidas para su conservación.

Compared to most other mammals, primates are relatively long-lived, endowed with relatively large brains, and characterized by slow life histories (van Schaik and Isler 2012), making them important and interesting subjects for comparative long-term field studies (Kappeler et al. 2012). Primates are comprised of 2 infraorders, Strepsirrhini and Haplorrhini; the former includes lemurs and lorises, the latter anthropoids (monkeys and apes) and tarsiers. Formerly, lemurs, lorises, and tarsiers together were referred to as “prosimians,” but it is now clear from molecular studies that they are not 1 group. Lemurs and lorises belong to Infraorder Strepsirrhini, and tarsiers (along with anthropoids) belong to Infraorder Haplorrhini (Schmitz et al. 2001). Although Strepsirrhines have some of the faster life histories among living primates, long-term research efforts are still necessary to unravel their diverse social, ecological, and life history adaptations. There are about 100 extant species of lemurs and 30 species of lorises (making up the suborder Strepsirrhini) plus 10 species of tarsiers (Groves 2001).

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

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

ECOPHYSIOLOGY

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

SOCIAL SYSTEMS

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

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

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

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

Asian lorises reveal complexity similar to the lemurs. In the Javan slow lorises (*Nycticebus javanicus)*, males begin to disperse at 14-18 months of age, slowly making forays from the home range. Female dispersal occurs slightly later and is more directed. Both sexes disperse 1-6 km away from their natal range, and dispersal may occur in stages whereby a young loris attempts to settle, and even pairs for ≤ 1 year with another loris before moving on again (Nekaris 2014). In spectral tarsiers, males disperse twice as far as females do (Gursky 2010b). As a result, only females regularly form territories adjacent to their parental ranges. The site fidelity of individuals that were relocated to their original sleeping tree 5 years later was positively related to the width (diameter at breast height) and height of their sleeping trees. Thus, diverse combinations of social and ecological factors appear to explain dispersal in different species of strepsirrhines and tarsiers, which exhibit deviations from the dominant mammalian pattern of male-only dispersal.

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

Social structure. — There are fundamental challenges for mammals that live in dispersed social networks. These networks are characterized by individualized stable associations and solitary foraging, and they require coordination of movements, cohesion, and reproduction in time and space, particulary if a species is sympatric with cryptic species of similar body mass. Long-term bioacoustic studies were done on individually marked lemurs of 4 species of the nocturnal lemur community in Ankarafantsika National Park (mouse lemurs, *M. murinus* and *M. ravelobensis;* Milne-Edwards's sportive lemur, *Lepilemur edwardsi*; and the western woolly lemur, *Avahi occidentalis)*, and it was found that different species exploit different acoustic niches for communication (Zimmermann 2016a). The 2 small-bodied species, the mouse lemurs, use the high frequency (ultrasonic) range as an adaptation to predation. This research also revealed a hitherto neglected role of acoustic signaling in governing group reunion and dispersal as well as species cohesiveness in sympatry, with cues from acoustic structure of the calls that characterize individual identity, sex, kinship, group, or species identity (Zimmermann 2016b). In *L. edwardsi*, pair partners engage in duetting at resource sites, supporting the notion that duetting evolved as a mechanism to coordinate activities between pair partners dispersed in space, to strengthen pair bonds, and to limit infanticide and nutritional stress in lactating females (Méndez-Cárdenas and Zimmermann 2009). Specific syllables within these duets also occur in alarm calls (Scheumann et al. 2007). Acoustic signaling in this nocturnal lemur community allows recognition, even across distance, and consequently gathering of dispersed group members at a particular site and a distinct time; vocal exchanges also help to limit costly, direct intra- and interspecific conflicts (Zimmermann 2016a, 2016b). Furthermore, specific differences in acoustic signaling facilitates the recognition of conspecifics and contribute to cohesiveness of species sympatric with other species (Braune et al. 2008; Zimmermann and Radespiel 2014).

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

POPULATION AND COMMUNITY ECOLOGY

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

Population dynamics. — Studies of population density and ranging can yield key information, both for conservation management and for understanding energetic strategies and constraints driving the evolution of social systems. Long-term variation in population abundance and distribution can be the result of species-specific habitat requirements or interspecific competition. Long-term ecological research over a period of more than 15 years at Ankarafantsika suggests that the heterogeneous distribution of *Microcebus* species there is most likely based on species-specific (micro-) habitat preferences related more to divergent patterns of resource use than to interspecific competition (Radespiel 2016). Competitive exclusion may also account for variation in population density in red-bellied lemurs (*Eulemur rubriventer*) and *E. rufifrons,* golden bamboo lemurs *(Hapalemur aureus*) and gray bamboo lemurs (*Hapalemur griseus*), as well as Peyrieras' woolly lemurs (*Avahi peyrierasi*) and the small-toothed sportive lemur (*Lepilemur microdon*) at Ranomafana (Wright et al. 2012).

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

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

Female *P. verreauxi* in the dry deciduous forests at Beza Mahafaly reach sexual maturity around 4 years, but fertility peaks between 7 and 17 years, dropping off after 17 years (Richard et al. 2002). This species is is long lived (Morris et al. 2011) and is characterized by slow rates of aging (Bronikowski et al. 2011). Relative to their body size, *P. verreauxi* reproduces later and lives longer (up to 19 years) than any other non-human primate species for which there are comparable data (Richard et al. 2002). Many demographic traits such as life expectancy, reproductive value (i.e., an individual's expected future contribution to population growth), and population growth rate exhibits lower values in periods when annual rainfall is low, and a stochastic demographic analysis also shows that population growth rate is depressed as the variance in annual rainfall increases (Lawler et al. 2009). These life history patterns are consistent with theoretical expectation and empirical findings pertaining to life history evolution in an unpredictable climatic environment (Dewar and Richard 2007). Similarly, in high (but still variable) rainfall areas such as Ranomafana, *P. edwardsi* has larger home ranges (50 ha) and lower population density, yet the trends of long lifespans (up to 30+ years) and slow development are consistent with data from other species of sifakas, both sympatric species and dry-forest species (Morelli et al. 2009; King et al. 2012; Tecot et al. 2013).

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

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

CONSERVATION

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

Long-term presence of researchers is also necessary to assess the feasibility and effectiveness of concrete conservation measures aimed at diminishing the effects of fragmentation, degradation, and possibilities of restoring connectivity between isolated habitats through corridors. Gray mouse lemurs are suitable candidates to address these issues because of their short generation time and high densities. Long-term monitoring reveals that they can use mixed tree plantations, including exotic tree species, as corridors within 5 years after being planted (Andriamandimbiarisoa et al. 2015). Slow lorises, too, have been shown to persist in agricultural plantations if suitable plant species are available (Nekaris 2014). The knowledge that introduced fast growing tree species can be used by lemurs and lorises offers new perspectives for restructuring fragmented landscapes for conservation. Long-term research coupled with conservation genetics can give us important insights into endangered species, providing better assessment of functional genetic diversity in the face of habitat fragmentation (Baden et al. 2014).

ADDITIONAL TOPICS

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

FUTURE DIRECTIONS

Long-term work on several populations of strepsirrhines and tarsiers has now been ongoing for several decades. The biggest challenge for successful continuation of these projects is the implementation of supportive frameworks in terms of political and economic stability in Madagascar and other range countries to allow them to continue. The other side of this coin pertains to the establishment of financial mechanisms for long-term sustainability of field sites in the countries where most of the researchers are currently based. Moreover, to understand fully the evolution and adaptations of these ecologically and socially diverse primate taxa, more long-term field studies are needed, especially on bushbabies (Galagidae; see Kotze et al. 2016) and pottos (*Perodicticus* species). Finally, long-term sites have generated rigorous long-term data, and merging them into a comparative and synthetic data base would now provide the ability to answer a number of big questions in primate biology. The present special feature provides an example of how such integration can be accomplished.

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SUPPLEMENTARY DATA

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

Supplementary data S2. – References cited in S1.

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Figure legend

Fig. 1. — Location of long-term lemur study sites in Madagascar. Inset shows location of Madagascar off SE coast of Africa.