



## Long-term field studies of lemurs, lorises, and tarsiers

PETER M. KAPPELER,\* FRANK P. CUOZZO, CLAUDIA FICHTEL, JÖRG U. GANZHORN, SHARON GURSKY-DOYEN, MITCHELL T. IRWIN, SHINICHIRO ICHINO, RICHARD LAWLER, K. ANNE-ISOLA NEKARIS, JEAN-BAPTISTE RAMANAMANJATO, UTE RADESPIEL, MICHELLE L. SAUTHER, PATRICIA C. WRIGHT, AND ELKE ZIMMERMANN

*Behavioral Ecology & Sociobiology Unit, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany (PMK, CF)*

*Dept. Sociobiology/Anthropology, Georg August University, Kellnerweg 6, Göttingen, Germany (PMK)*

*Dept. Biological Anthropology, University of North Dakota, Grand Forks, ND 58202, USA (FPC)*

*Dept. Ecology and Animal Conservation, Hamburg University, 20146 Hamburg, Germany (JUG)*

*Dept. Anthropology, Texas A&M University, College Station, TX 77843, USA (SG-D)*

*Dept. Anthropology, Northern Illinois University, DeKalb, IL 60115, USA (MTI)*

*Center for African Area Studies, Kyoto University, 606-8501 Kyoto, Japan (SI)*

*Dept. Anthropology, James Madison University, Harrisonburg, VA 22807, USA (RL)*

*Nocturnal Primate Research Group, Oxford Brookes University, Oxford, Ox3 OBP, United Kingdom (KA-IN)*

*QIT Madagascar Minerals, Tolagnaro, Madagascar (J-BR)*

*Institute of Zoology, University of Veterinary Medicine, 30559 Hannover, Germany (UR, EZ)*

*Biological Anthropology, University of Colorado, Boulder, CO 80309-0233, USA (MLS)*

*Institute for the Conservation of Tropical Environments, Stony Brook University, Stony Brook, NY 11794-4364, USA (PCW)*

\* Correspondent: [pkappel@gwdg.de](mailto:pkappel@gwdg.de)

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 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 for 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 monitoring of populations.

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 en Madagascar y una especie de loris y otra de tarsero, en Indonesia. Se resalta la importancia de las áreas de estudio a largo plazo como prerequisite esencial para planear y llevar a cabo estudios de menor duración sobre temas específicos, como lo ejemplifican varios estudios eco-fisiológicos en lemurs. Estudios a largo plazo de individuos conocidos, han revelado variación en la organización social dentro y entre especies ecológicamente similares. Incluso en estos primates, con un ciclo de vida relativamente corto, se necesita recopilar más de una década de datos de paternidad para determinar el sesgo reproductivo de los machos. Sin embargo, aún se sabe poco de las consecuencias a largo plazo que la posición de las hembras en la jerarquía social puede tener en su éxito reproductivo. El monitoreo a largo plazo de individuos conocidos es el único método para obtener datos sobre adaptaciones en su historia natural, las cuales aparentemente son

moduladas en función de la predación a las especies estudiadas en este trabajo. Estos estudios a largo plazo son también necesarios para afrontar temas específicos sobre la ecología de estas comunidades. La simple presencia de proyectos a largo plazo tienen un efecto positivo en la protección de los lugares de estudio, como así también generan datos únicos que son fundamentales para apoyar medidas de conservación tales como el monitoreo de poblaciones.

Key words: behavior, ecology, lemurs, lorises, tarsiers

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). 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 Suborder Strepsirrhini, and tarsiers (along with anthropoids) belong to Suborder 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, plus 10 species of tarsiers (Groves 2001). A number of new species of strepsirrhines and tarsiers have been discovered and described in the last decade, i.e., since the publication of Wilson and Reeder (2005). Species referred to below that fall into this category include the red-fronted brown lemur (*Eulemur rufifrons*), Peyrieras’s woolly lemur (*Avahi peyrierasi*), and the small-toothed sportive lemur (*Lepilemur microdon*—Mittermeier et al. 2008).

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 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 tarsier*—Groves et al. 2008) 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 potto (*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 SD1). 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

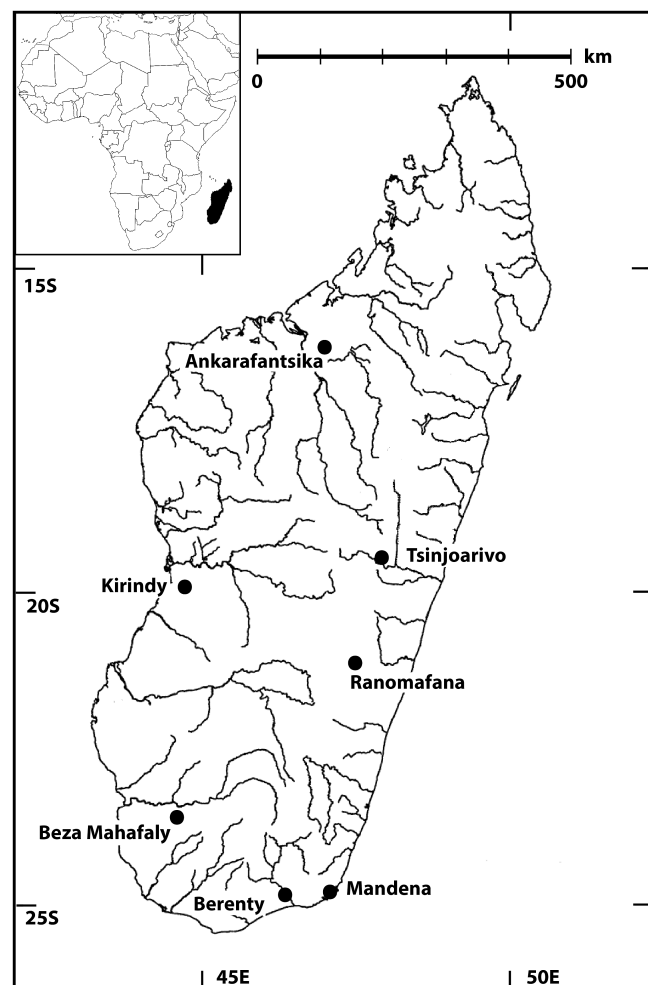


Fig. 1.—Location of long-term lemur study sites in Madagascar. Inset shows location of Madagascar off SE coast of Africa.

at long-term studies (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 Sautther 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 (*T. tarsier*), 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 ring-tailed lemurs (*Lemur catta*—Sussman 1992; Sautther 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 red-fronted brown lemurs (*E. 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  $\leq 1$  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-biased dispersal.

*Mating system.*—Long-term studies have informed our understanding of mating systems in lemurs, mainly with respect to reproductive strategies of males, which has emerged from genetic paternity data collected over a decade or more. For example, in *P. verreauxi*, mating occurs both within and between social 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 infants over more than 10 years, the greatest skew observed in male reproductive success in all primates (Kappeler and Schaffler



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, particularly 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 2016). The 2 small-bodied species, the mouse lemurs, use the high frequency (ultrasonic) range, presumably as an adaptation to reduce risk of 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, in press). 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 2016, in press). Furthermore, specific differences in acoustic signaling facilitate 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 at Ranomafana may also account for variation in population density in several closely related species pairs, including red-bellied lemurs (*Eulemur rubriventer*) and red-fronted brown lemurs (*E. rufifrons*), golden bamboo lemurs (*Hapalemur aureus*) and gray bamboo lemurs (*Hapalemur griseus*), and Peyrieras' woolly lemurs (*A. peyrierasi*) and small-toothed sportive lemurs (*L. microdon*) at Ranomafana (Wright et al. 2012).

For example, *P. diadema* in more-disturbed habitats at Tsinjoarivo have smaller home ranges 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 was 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 fossas (*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 the environment and life histories of lemurs 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 at around 4 years of age, but fertility peaks between 7 and 17 years, dropping off after 17 years (Richard et al. 2002). This species 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 exhibit 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 life spans (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 that is especially damaging in the fragmented forests at Tsinjoarivo, where it is unlikely that “empty” forest fragments will be recolonized because 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 defensive behaviors in males, suggesting that 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 (*Acrantophis 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 health of lemurs 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 also have 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 predation on vertebrates (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* spp.). 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.

### ACKNOWLEDGMENTS

We thank C. Schradin and L. Hayes for their invitation to contribute to this special issue and 2 referees for comments. Special thanks to C. Chapman for additional constructive comments and to E. Bernaldo de Quiros for translating the abstract. This paper is dedicated to the memory of R. Sussman (1941–2016), a pioneer of long-term lemur research.

### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Long-term studies (10 or more years) or those studies with the potential to become long-term studies.

### LITERATURE CITED

- ANDRIAMANDIMBIARISOA, L., ET AL. 2015. Habitat corridor utilization by the gray mouse lemur, *Microcebus murinus*, in the littoral forest fragments of south eastern Madagascar. *Madagascar Conservation & Development* 10:144–150.
- BADEN, A. L., S. M. HOLMES, S. E. JOHNSON, S. E. ENGBERG, E. E. LOUIS, AND B. J. BRADLEY. 2014. Species-level view of population structure and gene flow for a critically endangered primate (*Varecia variegata*). *Ecology and Evolution* 4:2675–2692.
- BLANCO, M. B., K. H. DAUSMANN, J. F. RANAIVOARISO, AND A. D. YODER. 2013. Underground hibernation in a primate. *Scientific Reports* 3:1768.
- BRAUNE, P., S. SCHMIDT, AND E. ZIMMERMANN. 2008. Acoustic divergence in the communication of cryptic species of nocturnal primates (*Microcebus* spp.). *BMC Biology* 6:19.
- BROCKMAN, D. K., A. K. COBDEN, AND P. L. WHITTEN. 2009. Birth season glucocorticoids are related to the presence of infants in sifaka (*Propithecus verreauxi*). *Proceedings of the Royal Society of London, B. Biological Sciences* 276:1855–1864.
- BROCKMAN, D. K., P. L. WHITTEN, A. F. RICHARD, AND B. BENANDER. 2001. Birth season testosterone levels in male Verreaux's sifaka, *Propithecus verreauxi*: insights into sociodemographic factors mediating seasonal testicular function. *Behavioral Ecology and Sociobiology* 49:117–127.
- BROCKMAN, D. K., P. L. WHITTEN, A. F. RICHARD, AND A. SCHNEIDER. 1998. Reproduction in free-ranging male *Propithecus verreauxi*: the hormonal correlates of mating and aggression. *American Journal of Physical Anthropology* 105:137–152.
- BRONIKOWSKI, A. M., ET AL. 2011. Aging in the natural world: comparative data reveal similar mortality patterns across primates. *Science* 331:1325–1328.
- CHARLES-DOMINIQUE, P. 1970. Evolution of lorises and lemurs. *Nature* 227:257–260.
- CLOUGH, D., M. HEISTERMANN, AND P. M. KAPPELER. 2010. Host intrinsic determinants and potential consequences of parasite infection in free-ranging red-fronted lemurs (*Eulemur fulvus rufus*). *American Journal of Physical Anthropology* 142:441–452.
- CUOZZO, F. P., AND M. L. SAUTHER. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. *Journal of Human Evolution* 51:490–505.
- DAMMHAHN, M., AND P. M. KAPPELER. 2009. Females go where the food is: does the socio-ecological model explain variation in social organisation of solitary foragers? *Behavioral Ecology and Sociobiology* 63:939–952.
- DEWAR, R. E., AND A. F. RICHARD. 2007. Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences* 104:13723–13727.
- DUNHAM, A. E., E. M. ERHART, AND P. C. WRIGHT. 2011. Global climate cycles and cyclones: consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. *Global Change Biology* 17:219–227.



- ERHART, E. M., AND D. J. OVERDORFF. 1998. Infanticide in *Propithecus diadema edwardsi* in southeastern Madagascar. *International Journal of Primatology* 19:53–72.
- FICHEL, C., C. KRAUS, A. GANSWINDT, AND M. HEISTERMANN. 2007. Influence of reproductive season and rank on fecal glucocorticoid levels in free-ranging male Verreaux's sifakas (*Propithecus verreauxi*). *Hormones and Behavior* 51:640–648.
- GÉNIN, F. 2010. Who sleeps with whom? Sleeping association and socio-territoriality in *Microcebus griseorufus*. *Journal of Mammalogy* 91:942–951.
- GOULD, L., R. W. SUSSMAN, AND M. L. SAUTHER. 1999. Natural disasters and primate populations: the effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. *International Journal of Primatology* 20:69–84.
- GROVES, C. P. 2001. Primate taxonomy. Smithsonian Institution Press, Washington, D.C.
- GROVES, C. P., SHEKELLE, M., AND D. BRANDON-JONES. 2008. Taxonomic history of the tarsiers, evidence for the origins of Buffon's tarsier, and the fate of *Tarsius spectrum* Pallas, 1778. Pp. 1–12 in *Primates of the oriental night* (M. Shekelle, I. Maryanto, and C. Groves, eds.). LIPI Press, West Java, Indonesia.
- GURSKY, S. L. 1995. Group size and composition in the spectral tarsier: implications for social organization. *Tropical Biodiversity* 3:57–62.
- GURSKY, S. L. 2005. Predator mobbing in *Tarsius spectrum*. *International Journal of Primatology* 26:207–221.
- GURSKY, S. L. 2010a. Intraspecific variation in the mating system of spectral tarsiers. *International Journal of Primatology* 31:1161–1173.
- GURSKY, S. L. 2010b. Dispersal patterns in *Tarsius spectrum*. *International Journal of Primatology* 31:117–131.
- HÄMÄLÄINEN, A. 2012. A case of adult cannibalism in the gray mouse lemur, *Microcebus murinus*. *American Journal of Primatology* 74:783–787.
- HÄMÄLÄINEN, A., ET AL. 2014. Senescence or selective disappearance? Age trajectories of body mass in wild and captive populations of a small-bodied primate. *Proceedings of the Royal Society of London, B. Biological Sciences* 281:20140830.
- HANNAH, L., ET AL. 2008. Climate change adaptation for conservation in Madagascar. *Biology Letters* 4:590–594.
- HARPER, G. J., M. K. STEININGER, C. J. TUCKER, D. JUHN, AND F. HAWKINS. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation* 34:325–333.
- HLADIK, C. M., M. PINTE, AND B. SIMMEN. 1998. Les densités de population des prosimiens nocturnes du sud de Madagascar varient-elles à long terme dans les réserves forestières accessibles au public? *Revue d'Ecologie (Terre Vie)* 53:181–185.
- ICHINO, S. 2006. Troop fission in wild ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. *American Journal of Primatology* 68:97–102.
- ICHINO, S., AND N. KOYAMA. 2006. Social changes in a wild population of ringtailed lemurs (*Lemur catta*) at Berenty, Madagascar. Pp. 233–244 in *Ringtailed lemur biology* (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.
- ICHINO, S., AND H. RAMBELOARIVONY. 2011. New cases of vertebrate predation by the ring-tailed lemur (*Lemur catta*), with reference to differences from *Eulemur* species and other primates. *African Study Monographs* 32:69–80.
- ICHINO, S., ET AL. 2015. Lifespan and reproductive senescence in a free-ranging ring-tailed lemur (*Lemur catta*) population at Berenty, Madagascar. *Folia Primatologica* 86:134–139.
- IRWIN, M. T. 2008. Diademed sifaka (*Propithecus diadema*) ranging and habitat use in continuous and fragmented forest: higher density but lower viability in fragments? *Biotropica* 40:231–240.
- IRWIN, M. T., R. E. JUNGE, J.-L. RAHARISON, AND K. E. SAMONDS. 2010. Variation in physiological health of diademed sifakas across intact and fragmented forest at Tsinjoarivo, eastern Madagascar. *American Journal of Primatology* 72:1013–1025.
- IRWIN, M. T., J. L. RAHARISON, AND P. C. WRIGHT. 2009. Spatial and temporal variability in predation on rainforest primates: do forest fragmentation and predation act synergistically? *Animal Conservation* 12:220–230.
- JOLLY, A. 2012. Berenty Reserve, Madagascar: a long time in a small space. Pp. 21–44 in *Long-term field studies of primates* (P. M. Kappeler and D. P. Watts, eds.). Springer, Heidelberg, Germany.
- JOLLY, A., AND E. PRIDE. 1999. Troop histories and range inertia of *Lemur catta* at Berenty, Madagascar: a 33-year perspective. *International Journal of Primatology* 20:359–373.
- JOLLY, A., ET AL. 2000. Infant killing, wounding and predation in *Eulemur* and *Lemur*. *International Journal of Primatology* 21:21–40.
- JOLLY, A., ET AL. 2002. Demography of *Lemur catta* at Berenty Reserve, Madagascar: effects of troop size, habitat and rainfall. *International Journal of Primatology* 23:327–353.
- KAPPELER, P. M. 2012. The behavioral ecology of strepsirrhines and tarsiers. Pp. 17–42 in *The evolution of primate societies* (J. C. Mitani, J. Call, P. M. Kappeler, R. Palombit, and J. B. Silk, eds.). University of Chicago Press, Chicago, Illinois.
- KAPPELER, P. M., AND C. FICHEL. 2012a. A 15-year perspective on the social organization and life history of sifaka in Kirindy Forest. Pp. 101–121 in *Long-term field studies of primates* (P. M. Kappeler and D. P. Watts, eds.). Springer, Heidelberg, Germany.
- KAPPELER, P. M., AND C. FICHEL. 2012b. Female reproductive competition in *Eulemur rufifrons*: eviction and reproductive restraint in a plurally breeding Malagasy primate. *Molecular Ecology* 21:685–698.
- KAPPELER, P. M., AND C. FICHEL. 2015. Eco-evo-devo of the lemur syndrome: did adaptive behavioral plasticity get canalized in a large primate radiation? *Frontiers in Zoology* 12:S15.
- KAPPELER, P. M., AND M. PORT. 2008. Mutual tolerance or reproductive competition? Patterns of reproductive skew among male red-fronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology* 62:1477–1488.
- KAPPELER, P. M., AND L. SCHÄFFLER. 2008. The lemur syndrome unresolved: extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance. *Behavioral Ecology and Sociobiology* 62:1007–1015.
- KAPPELER, P. M., AND C. P. VAN SCHAIK. 2002. Evolution of primate social systems. *International Journal of Primatology* 23:707–740.
- KAPPELER, P. M., C. P. VAN SCHAIK, AND D. P. WATTS. 2012. The values and challenges of long-term field studies. Pp. 3–18 in *Long-term field studies of primates* (P. M. Kappeler and D. P. Watts, eds.). Springer, Heidelberg, Germany.
- KARPANTY, S. M. 2006. Direct and indirect impacts of raptor predation on lemurs in Southeastern Madagascar. *International Journal of Primatology* 27:239–261.
- KARPANTY, S. M., AND P. C. WRIGHT. 2007. Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments. Pp. 77–99 in *Primates and their predators* (S. L. Gursky and K. A. I. Nekaris, eds.). Springer Press, New York.
- KING, S. J., ET AL. 2012. Lemur habitat and dental senescence in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology* 148:228–237.

- KOBBE, S., J. U. GANZHORN, AND K. DAUSMANN. 2011. Extreme individual flexibility of heterothermy in free-ranging Malagasy mouse lemurs (*Microcebus griseorufus*). *Journal of Comparative Physiology B* 181:165–173.
- KOTZE, A., D. L. DALTON, M. STRINDEN, M. L. SAUTHER, F. P. CUOZZO, AND A. C. STONE. 2016. An evaluation of the oral microbiome and potential zoonoses of the southern thick-tailed or treater galago (*Otolemur crassicaudatus*). *African Primates* 11:19–26.
- KOYAMA, N. 1991. Troop division and inter-troop relationships of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. Pp. 173–176 in *Primateology today* (A. Ehara, T. Kimura, O. Takenaka, and M. Iwamoto, eds.). Elsevier, Amsterdam, The Netherlands.
- KOYAMA, N., S. ICHINO, M. NAKAMICHI, AND Y. TAKAHATA. 2005. Long-term changes in dominance ranks among ring-tailed lemurs at Berenty Reserve, Madagascar. *Primates* 46:225–234.
- KOYAMA, N., M. NAKAMICHI, R. ODA, N. MIYAMOTO, S. ICHINO, AND Y. TAKAHATA. 2001. A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. *Primates* 42:1–14.
- KOYAMA, N., T. SOMA, S. ICHINO, AND Y. TAKAHATA. 2006. Home ranges of ringtailed lemur troops. Pp. 86–101 in *Ringtailed lemur biology* (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.
- KUBZDELA, K. 1997. Feeding competition and reproductive success in the white sifaka (*Propithecus verreauxi verreauxi*). Ph.D. dissertation, University of Chicago, Chicago, Illinois.
- LAHANN, P., J. SCHMID, AND J. U. GANZHORN. 2006. Geographic variation in life history traits of *Microcebus murinus* in Madagascar. *International Journal of Primatology* 27:983–999.
- LAWLER, R. R. 2007. Fitness and extra-group reproduction in male Verreaux's sifaka (*Propithecus verreauxi verreauxi*). *American Journal of Physical Anthropology* 132:267–277.
- LAWLER, R. R., H. CASWELL, A. F. RICHARD, J. RATSIRARSON, R. E. DEWAR, AND M. SCHWARTZ. 2009. Demography of Verreaux's sifaka in a stochastic rainfall environment. *Oecologia* 161:491–504.
- LAWLER, R. R., A. F. RICHARD, AND M. A. RILEY. 2005. Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). *Journal of Human Evolution* 48:259–277.
- LOUDON, J. E., AND M. L. SAUTHER. 2013. Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemur (*Lemur catta*) endoparasitism at the Beza Mahafaly Special Reserve, Madagascar. *Conservation and Development* 8:21–28.
- LUTERMANN, H., B. SCHMELTING, U. RADESPIEL, P. EHRESMANN, AND E. ZIMMERMANN. 2006. The role of survival for the evolution of female philopatry in a solitary forager, the grey mouse lemur (*Microcebus murinus*). *Proceedings of the Royal Society of London, B. Biological Sciences* 273:2527–2533.
- MÉNDEZ-CÁRDENAS, M., AND E. ZIMMERMANN. 2009. Duetting – a mechanism to strengthen pair bonds in a dispersed pair-living primate (*Lepilemur edwardsi*)? *American Journal of Physical Anthropology* 139:523–532.
- MITTERMEIER, R. A., ET AL. 2008. Lemur diversity in Madagascar. *International Journal of Primatology* 29:1607–1656.
- MORELLI, T. L., S. J. KING, S. T. POCHRON, AND P. C. WRIGHT. 2009. The rules of disengagement: takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. *Behaviour* 146:499–523.
- MORRIS, W. F., ET AL. 2011. Low demographic variability in wild primate populations: fitness impacts of variation, covariation, and serial correlation in vital rates. *American Naturalist* 177:e14–28.
- NEKARIS, K. A. I. 2014. Extreme primates: ecology and evolution of Asian lorises. *Evolutionary Anthropology* 23:177–187.
- OVERDORFF, D. J., A. M. MERENLENDER, P. TALATA, A. TELO, AND Z. A. FORWARD. 1999. Life history of *Eulemur fulvus rufus* from 1988–1998 in southeastern Madagascar. *American Journal of Physical Anthropology* 108:295–310.
- PARGA, J. A., ET AL. 2015. Genetic evidence for male and female dispersal in wild *Lemur catta*. *Folia Primatologica* 86:66–75.
- PETTER, J.-J. 1962. Ecological and behavioral studies of Madagascar lemurs in the field. *Annals of the New York Academy of Sciences* 102:267–281.
- POCHRON, S. T., ET AL. 2003. Patterns of female dominance in *Propithecus diadema edwardsi* of Ranomafana National Park, Madagascar. *American Journal of Primatology* 61:173–185.
- POCHRON, S. T., TUCKER W. T., AND WRIGHT P. C. 2004. Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986–2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology* 125:61–72.
- PRIDE, R. E. 2005. Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology* 16:550–560.
- RABESANDRATANA, A. Z., RAKOTONDRAVONY, R., AND E. ZIMMERMANN. 2012. Distribution and abundance of the Milne Edwards' sportive lemur *Lepilemur edwardsi* in the Ankarafantsika National Park, northwestern Madagascar. *Lemur News* 16:57–60.
- RADESPIEL, U. 2006. Ecological diversity and seasonal adaptations of mouse lemurs (*Microcebus* spp.). Pp. 211–233 in *Lemurs: ecology and adaptation* (L. Gould and M. L. Sauther, eds.). Springer, New York.
- RADESPIEL, U. 2016. Can behavioral ecology help to understand the divergent geographic range sizes of mouse lemurs? Pp. 498–519 in *Gremlins of the night: biology, behavior, and conservation biogeography of the Cheirogaleidae* (S. M. Lehman, U. Radespiel, and E. Zimmermann, eds.). Cambridge University Press, Cambridge, United Kingdom.
- RADESPIEL, U., M. JURIĆ, AND E. ZIMMERMANN. 2009. Sociogenetic structures, dispersal and the risk of inbreeding in a small nocturnal lemur, the golden-brown mouse lemur (*Microcebus ravelobensis*). *Behaviour* 146:607–628.
- RADESPIEL, U., K. SCHABER, S. E. KESSLER, F. SCHAARSCHMIDT, AND C. STRUBE. 2015. Variations in the excretion patterns of helminth eggs in two sympatric mouse lemur species (*Microcebus murinus* and *M. ravelobensis*) in northwestern Madagascar. *Parasitology Research* 114:941–954.
- RASOLOHARIJAONA, S., RAKOTOSAMIMANANA, B., AND E. ZIMMERMANN. 2000. Infanticide by a male Milne-Edwards' sportive lemur (*Lepilemur edwardsi*) in Ampijoroa, NW-Madagascar. *International Journal of Primatology* 21:41–45.
- RICHARD, A. F. 1992. Aggressive competition between males, female-controlled polygyny, and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. *Journal of Human Evolution* 22:395–406.
- RICHARD, A. F., R. E. DEWAR, M. SCHWARTZ, AND J. RATSIRARSON. 2002. Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology (London)* 256:421–436.
- RICHARD, A. F., P. RAKOTOMANGA, AND M. SCHWARTZ. 1993. Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar: 1984–1991. *American Journal of Primatology* 30:1–20.
- SAUTHER, M. L., AND F. P. CUOZZO. 2009. The impact of fallback foods on wild ring-tailed lemur biology: a comparison of intact and anthropogenically disturbed habitat. *American Journal of Physical Anthropology* 140:671–686.



- SAUTHER, M. L., R. W. SUSSMAN, AND L. GOULD. 1999. The socioecology of the ringtailed lemur: thirty-five years of research. *Evolutionary Anthropology* 8:120–132.
- SCHEUMANN, M., A. RABESANDRATANA, AND E. ZIMMERMANN. 2007. Predation, communication, and cognition in lemurs. Pp. 100–126 in *Primate anti-predator strategies* (S. L. Gursky and K. A. I. Nekar, eds.). Springer, New York.
- SCHMELTING, B., E. ZIMMERMANN, O. BERKE, M. W. BRUFORD, AND U. RADESPIEL. 2007. Experience-dependent recapture rates and reproductive success in male grey mouse lemurs (*Microcebus murinus*). *American Journal of Physical Anthropology* 133:743–752.
- SCHMID, J., AND P. M. KAPPELER. 1994. Sympatric mouse lemurs (*Microcebus* spp.) in western Madagascar. *Folia Primatologica* 63:162–170.
- SCHMID, J., AND P. M. KAPPELER. 2005. Physiological adaptations to seasonality. Pp. 129–155 in *Primate seasonality: implications for human evolution* (D. K. Brockman and C. P. van Schaik, eds.). Cambridge University Press, Cambridge, United Kingdom.
- SCHMITZ, J., M. OHME, AND H. ZISCHLER. 2001. SINE insertions in cladistic analyses and the phylogenetic affiliations of *Tarsius bancanus* to other primates. *Genetics* 157:777–784.
- SCHNOELL, A. V., M. DITTMANN, AND C. FICHTEL. 2014. Human-introduced long-term traditions in wild redfronted lemurs? *Animal Cognition* 17:45–54.
- SCHWITZER, C., ET AL. 2014. Averting lemur extinctions amid Madagascar's political crisis. *Science* 343:842–843.
- SIMMEN, B., ET AL. 2006. Plant species fed on by *Lemur catta* in gallery forests of the southern domain of Madagascar. Pp. 55–68 in *Ringtailed lemur biology* (A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds.). Springer, New York.
- SINGLETON, C. L., A. M. NORRIS, M. L. SAUTHER, F. P. CUOZZO, AND I. A. YOUSOUF JACKY. 2015. Ring-tailed lemur (*Lemur catta*) health parameters across two habitats with varied levels of human disturbance at the Bezà Mahafaly Special Reserve, Madagascar. *Folia Primatologica* 86:56–65.
- SPRINGER, A., M. MELLMANN, A. C. FICHTEL, AND P. M. KAPPELER. 2016. Social structure and *Escherichia coli* sharing in a group-living wild primate, Verreaux's sifaka. *BMC Ecology* 16:6.
- SUSSMAN, R. W. 1992. Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 13:395–413.
- TAKAHATA, Y., N. KOYAMA, S. ICHINO, N. MIYAMOTO, M. NAKAMICHI, AND T. SOMA. 2008. The relationship between female rank and reproductive parameters of the ringtailed lemur: a preliminary analysis. *Primates* 49:135–138.
- TECOT, S. B. GERBER, S. J. KING, J. VERDOLIN, AND P. C. WRIGHT. 2013. Risky business: sex differences in mortality and dispersal in a polygynous, monomorphic lemur. *Behavioral Ecology* 24:987–996.
- VAN SCHAİK, C. P., AND K. ISLER. 2012. Life-history evolution. Pp. 220–244 in *The evolution of primate societies* (J. C. Mitani, J. Call, P. M. Kappeler, R. Palombit, and J. B. Silk, eds.). University of Chicago Press, Chicago, Illinois.
- WEIDT, A., N. HAGENAH, B. RANDRIANAMBININA, U. RADESPIEL, AND E. ZIMMERMANN. 2004. Social organization of the golden brown mouse lemur (*Microcebus ravelobensis*). *American Journal of Physical Anthropology* 123:40–51.
- WILSON, D. E., AND D. M. REEDER. 2005. *Mammals of the world*. 3rd ed. The Johns Hopkins University Press, Baltimore, Maryland.
- WRIGHT, P. C. 1999. Lemur traits and Madagascar ecology: coping with an island environment. *Yearbook of Physical Anthropology* 42:31–72.
- WRIGHT, P. C., ET AL. 2008a. The crisis of the critically endangered greater bamboo lemur (*Prolemur simus*). *Primate Conservation* 23:11–22.
- WRIGHT, P. C., S. J. KING, A. BADEN, AND J. JERNVALL. 2008b. Aging in wild female lemurs: sustained fertility with increased infant mortality. Pp. 17–28 in *Primate reproductive aging: cross-taxon perspectives* (S. Atsalis, S. W. Margulis, and P. R. Hof, eds.). Karger Press, Basel, Switzerland.
- WRIGHT, P. C., ET AL. 2009. Habitat disturbance and seasonal fluctuations of lemur parasites in the rain forest of Ranomafana National Park, Madagascar. Pp. 311–330 in *Primate parasite ecology: the dynamics and study of host-parasite relationships* (M. A. Huffman and C. A. Chapman, eds.). Cambridge University Press, Cambridge, United Kingdom.
- WRIGHT, P. C., ET AL. 2012. Long-term lemur research at Centre Valbio, Ranomafana National Park, Madagascar. Pp. 67–100 in *Long-term field studies of primates* (P. M. Kappeler, and D. P. Watts, eds.). Springer, Heidelberg, Germany.
- WRIGHT, P. C., B. R. ANDRIAMIHAJA, S. J. KING, J. GUERRIERO, AND J. HUBBARD J. 2014. Lemurs and tourism in Ranomafana National Park, Madagascar: economic boom and other consequences. Pp. 123–145 in *Primate-focused tourism* (A. Russon and J. Wallis J., eds.). Cambridge University Press, Cambridge, United Kingdom.
- ZIMMERMANN, E. 2016. Acoustic divergence in communication of cheirogaleids with special emphasis to mouse lemurs. Pp. 405–421 in *Gremlins of the night: biology, behavior, and conservation biogeography of the cheirogaleidae* (S. M. Lehman, U. Radespiel, and E. Zimmermann, eds.). Cambridge University Press, Cambridge, United Kingdom.
- ZIMMERMANN, E. In press. Evolutionary origins of primate vocal communication: diversity, complexity and flexibility of voices in strepsirrhines and tarsiers. In *Springer Handbook of Auditory Research: Primate Hearing and Communication* (R. Quam, M. Ramsier, R. R. Fay, and N. Popper, eds.). Springer, Heidelberg, Germany.
- ZIMMERMANN, E., S. CEPK, N. RAKOTOARISON, V. ZIEMANN, AND U. RADESPIEL. 1998. Sympatric mouse lemurs in north-west Madagascar: a new rufous mouse lemur species (*Microcebus ravelobensis*). *Folia Primatologica* 69:106–114.
- ZIMMERMANN, E., AND U. RADESPIEL. 2014. Species concepts, diversity, and evolution in primates: lessons to be learned from mouse lemurs. *Evolutionary Anthropology* 23:11–14.
- ZOHDY, S., I. R. FRIED, K. C. CROSS, P. C. WRIGHT, AND T. R. GILLESPIE. 2015. Diversity and prevalence of diarrhea-associated viruses in the lemur community and associated human population of Ranomafana National Park, Madagascar. *International Journal of Primatology* 36:143–153.

*Special Feature Editor was Barbara H. Blake.*