Long-term simian research sites: significance for theory and conservation

Colin A. Chapman,* Amélie Corriveau, Valérie A. M. Schoof, Dennis Twinomugisha, and Kim Valenta

Department of Anthropology and McGill School of Environment, McGill University, 855 Sherbrooke Street West, Montréal, Québec H3A 2T7, Canada (CAC, AC, VAMS, KV)
Department of Multidisciplinary Studies, Bilingual Biology Program, Glendon Campus, York University, 2275 Bayview Avenue, Toronto, Ontario M4N 3M6, Canada (VAMS)
Department of Zoology, Makerere University, P.O. Box 7062, Kampala, Uganda (DT)

* Correspondent: Colin.Chapman@McGill.ca

Simian primates (monkeys and apes) are typically long-lived animals with slow life histories. They also have varying social organization and can slowly impact their environment by either being seed dispersers or by overbrowsing their food trees. As a result, short-term studies and those focusing on just 1 location only provide a snapshot of simian life under a specific set of ecological conditions that typically do not represent the complete spatial and temporal picture. Long-term field studies are needed to obtain a true understanding of their behavior, life history, ecology, and the selective pressures acting on them. Fortunately, there have been many long-term studies of simians, so a great deal is known about many species. Here, we consider examples of long-term studies that have operated continuously for approximately a decade or more. We review studies that deal with ecophysiology, social organization, population and community ecology, or conservation. The information emerging from these sites is particularly helpful in the construction of informed conservation plans, which are desperately needed given the severity of threats to simians and the fact that responses do not occur over the duration of a Ph.D. or granting cycle (typically 1–3 years).

Key words: conservation, conservation planning, diet, ecophysiology, ecosystem engineers, hormones, life history, population and community processes, seed dispersal, social systems

Simians are long-lived mammals. For example, spider monkeys (*Ateles*) and chimpanzees (*Pan troglodytes*) can live up to 60 years (Chapman and Chapman 1990), have groups that can be very flexible over short spatial and temporal scales (Butynski 1990; Kappeler et al. 2013), and have intrigued researchers since they were first studied (Carpenter 1964). However, primatologists quickly recognized that the time frame of the typical study (1–3 years) did not reveal the complexity and flexibility inherent in simian behavior. For example, animals change dominance status repeatedly over time and may live in a number of groups (Chapman and Rothman 2009). Thus, a tradition developed that encouraged long-term field studies, which at some sites has extended over 3 generations of researchers (Table 1; Supplementary Data SD1). Recently, the need for long-term studies has taken on more urgency because anthropogenic influences are changing simian environments and conservation biologists need to understand

simian responses to these changes to design effective conservation and management plans.

The only way to understand how simians and other mammals are responding to these changes is through long-term research that documents changes in many ecological, physiological, and behavioral variables over a significant duration of the life of an individual and preferentially over several generations. Since there have been a number of recent reviews of long-term studies of apes, we limit our review to monkeys; prosimians are covered in the article by Kappeler et al. (this issue). Therefore, our objective is to examine data resulting from long-term studies of simians with respect to ecophysiology, social organization (Kappeler and van Schaik 2002), and population and community processes, and to evaluate how changes in these factors could influence the conservation of different species. For example, Bronikowski and Altmann (1996) used 10 years of data on behavior, ecology, rainfall, and

Table 1.—Advantages and significance of long-term field studies on primates.

Factor	Advantages and significance
Life history studies	Allow documentation of the fitness values of specific life history and behavioral strategies
	Facilitate documentation of individual fitness if the study is of sufficient duration (i.e., < 60 years)
Informing short-term studies	Identify importance of rare ecological pressures (e.g., disease) on behavior and population dynamics
	Illustrate if short-term studies are general
Documenting environmental variation	Provide an understanding of environmental variation and the strength of different selective pressures
	Illustrate variation in diet and social organization
	Document the extremes of dietary flexibility
Evolutionary importance of extreme events	Identify if extreme events are important selective pressures of determinants of population size
	Identify fallback foods and essential foods
Population and community ecology	Document forest change and the impact on simian behavior and population size
	Identify social drivers of behavior and life history strategies that are independent of ecology
	Quantify the impacts of climate change
	Quantify the impacts of anthropogenic change and the time needed for ecosystem and simian population recovery

temperature to document plasticity in foraging behavior of the baboon (*Papio cynocephalus*) and showed that responses to environmental variation differed among groups in ways that led to differences in conservation risks (see also Milton et al. 2005; Milton and Giacalone 2014). Such differences among groups in single populations are probably widespread among simians, but confirming their existence depends on comparably extensive long-term data sets.

Primates are a fascinating group of species and studying them provides remarkably unparalleled insights into the complexity of animal behavior, the evolution of complex social organization, and cognition. Furthermore, given the attention they get from the public, they are often flagship species for conservation. Decades of long-term field studies revealed numerous important insights into the social behavior, ecophysiology, and population dynamics of primates that contributed to their conservation. Here, we present examples of important findings from long-term primate research (largely excluding apes and prosimians—evaluated elsewhere, see below) to demonstrate the unique importance of long-term field studies to advance the field of mammalogy and theoretical biology in general. This is not meant to be a comprehensive review and we apologize in advance to those important studies and researchers we have not mentioned here. At least 95 long-term studies have been conducted on more than 66 species (25 focused on nonhuman great apes—*Pan*, *Gorilla*, and *Pongo*), and these numbers do not include studies on prosimians or those that studied the entire community (Supplementary Data SD1). In this review, we cannot cover the entire diversity of topics investigated but focus on ecophysiology, social organization, population and community ecology, and conservation. It should be noted that there is an absence of data on nocturnal species, but see Fernandez-Duque (2007) and Fernandez-Duque et al. (2008).

ECOPHYSIOLOGY

Given the logistic difficulty and cost, the majority of studies on ecophysiology have been short term, but some researchers have taken on the challenge of long-term ecophysiological research and these studies have focused on nutritional ecology and examining reproductive and stress hormones. Until the recent development of noninvasive sampling methods, the difficulties of capturing and anaesthetizing simians have impeded ecophysiological research, particularly for arboreal species.

Waterman et al. (1988) suggested that the biomass of folivorous colobines could be predicted by the weighted contributions of the protein-to-fiber ratio of mature leaves of the most abundant trees. Subsequently, this index of dietary quality has been successfully applied to predict the biomass of small-bodied folivorous monkeys at local (Chapman et al. 2002a; Ganzhorn 2002) and regional scales (Waterman et al. 1988; Oates et al. 1990; Davies 1994; Chapman et al. 2004; Fashing et al. 2007). These studies have led to investigations of the impact of climate change. Greenhouse experiments demonstrate that changes in temperature and rainfall, along with elevated CO_2, are expected to impact the nutritional quality of leaves. Thirty years of research have shown a decline in the quality of tropical tree leaves in Kibale (Rothman et al. 2015).

The refinement of techniques to assess hormonal metabolites from feces and urine has led to an upsurge in studies of physiology. Several long-term field projects have examined hormonal correlates of ecological and social factors (Santa Rosa Capuchin Project—Fedigan and Jack 2012; Kibale Chimpanzee Projects—Muller and Wrangham 2004; Gunung Palung Orangutan Project—Knott 1998). However, these long-term studies have only used these tools to assess physiology to address specific questions and have not monitored the physiological parameters over extensive periods. One notable exception is the Amboseli Baboon Research Project in Kenya, which has made extensive use of hormonal data since the development of this technique for the field. Though the project began in 1971, it was not until 2000 that the development and refinement of extraction techniques for fecal steroid metabolites allowed Jeanne Altmann and Susan Alberts to begin collecting longitudinal hormone data. The individual-based studies of the Amboseli baboons have resulted in some very interesting, and often surprising, findings on environmental responses, development, and socio-endocrinology of these simians (Gesquiere et al. 2005; Alberts and Altmann 2012; Franz et al. 2015).

The importance of food resources for reproduction has resulted in extensive research on the influence of environmental variation on simian reproductive physiology and reproduction, though variation in food availability, rainfall, and temperature may also affect males. Over an 8-year period, Gesquiere et al. (2011) examined male fecal glucocorticoids (fGC; hormones associated with energetic or psychosocial stress) of baboons in the highly variable and challenging habitat in Amboseli, National Park, Kenya. Male baboons had elevated fGC levels in the dry season, when the absence of rainfall is associated with progressive decreases in food and water availability compared to the wet season. This ecological stress may constrain

male reproduction given that in the dry season males also had lower fecal testosterone (fT) levels, a hormone associated with spermatogenesis and male reproductive effort. Despite lower fT levels during periods of extreme heat, there was no influence on fGC, indicating that temperature may affect fT directly rather than via suppression from elevated stress. In contrast, a shorter 5-year study on females indicated that fGC levels were higher in the dry season and during periods of extreme heat (Gesquiere et al. 2008). A similar but much shorter 17-month study on white-faced capuchin monkeys (*Cebus capucinus*) indicated a negative relationship between male fGC, but not fT, and fruit biomass and rainfall. Additionally, photoperiod was the best predictor of both fGC and fT, possibly because photoperiod in a given month is strongly correlated with both nonsocial and social environmental (e.g., seasonal increases in female ovulation) factors in the following month (Schoof et al. 2016). Among females, fGC levels were higher during the lean dry season compared to the wet season, though reproductive state and periods of instability in male rank also influenced fGCs (Carnegie et al. 2011).

Like many simians, baboons live in groups in which individuals can be ranked into dominance hierarchies, with high-ranking males generally benefiting from improved reproductive success. Whether or not these benefits are associated with additional costs is unclear. A 9-year study yielded surprising results on rank-related differences in fT and fGC and the influence of hierarchy stability (Gesquiere et al. 2011). Perhaps not surprisingly, high-ranking males had higher fT levels than low-ranking males, regardless of hierarchy stability. Generally speaking, there was also a negative relationship between rank and stress, with lower-ranking individuals exhibiting higher fGC levels. Alpha males are a remarkable exception as they exhibited higher fGC levels than 2nd-ranking beta males regardless of hierarchy stability. In this species, alpha male tenure is short, dominance is maintained agonistically, and alpha males spend a significant amount of time guarding fertile females. These activities are likely energetically costly, supporting the hypothesis that investment in dominance and reproductive effort by alpha males comes at a cost. Nonetheless, the authors still found some support for a potential cost of subordination, since the lowest-ranking males had the highest glucocorticoid levels, possibly as a result of limited access to food resources leading to energetic stress (Gesquiere et al. 2011). Among white-faced capuchins, where coresident males are tolerant, affiliative, have low rates of agonism, and an egalitarian mating system, alpha males who sire the majority of offspring (reviewed in Fedigan and Jack 2012) have higher fT and fGC levels than subordinate adult and subadult males (Schoof et al. 2014). In contrast, there is no relationship between female dominance rank and fGC (Carnegie et al. 2011).

SOCIAL ORGANIZATION

Long-term studies of simian social organization are the area where research on simians has contributed the most to our understanding of mammals and the development of widely applicable theories. Theory developed from studies on simians suggests that different types of feeding competition will lead to differences in social organization and structure (Wrangham 1980; van Schaik 1989; Sterck et al. 1997). The nature of the spatial and temporal distribution of food resources governs the level and type of feeding competition. Scramble competition involves the common depletion of food resources, whereas contest competition includes aggression, displacement, and avoidance within and between groups over access to monopolizable food sources (Nicholson 1933; Janson and van Schaik 1988). Animals must compete for food resources when the resources are limited, patchy and depletable, variable in quality, or monopolizable (Janson and van Schaik 1988; Isbell 1991; Chapman et al. 1995; Saj et al. 2007). Whenever only scramble competition occurs, or if there is no competition for food and food is not monopolizable, females are not expected to engage in agonistic interactions over food (Snaith and Chapman 2007, 2008), leading to an absence of linear dominance hierarchies and infrequent coalitions (Sterck et al. 1997). These patterns should co-occur with female dispersal because coalition partners are not required in feeding competition and female agonistic relationships should be rare, as will be female–female affiliative relationships. In contrast, when food resources are limited, patchy, depletable, and monopolizable, contest competition will occur and it becomes advantageous for females to have kin as allies in food defense. Accordingly, female dispersal should not occur. Initially, folivores were considered not to be food limited. This idea stemmed from the assumption that leaves are superabundant in forest habitats. However, many studies have recently demonstrated that folivorous simians are very selective in what they eat, typically preferring young leaves of just a few species (Chapman and Chapman 2002; Koenig and Borries 2006). These studies indicate that folivores may have different competitive regimes than previously thought (Snaith and Chapman 2005, 2007).

Studies concerning socioecology are common because understanding variation in social organizations of simians has been a central theme since the 1st field studies were initiated (Carpenter 1964; Gartlan and Brian 1968; Eisenberg et al. 1972; Struhsaker and Leland 1979; Wrangham 1980; Terborgh 1983). These early studies attempted to derive general frameworks of social organizations and group size but had few studies to draw information from; thus, species or genera were placed in categories based on the "average" behavioral characters for each taxonomic unit, ignoring within-species variation in social organizations. In recent years, it has become apparent that it is necessary to examine how different ecological pressures can lead to within-species variation in social organization (Chapman and Chapman 1999; Chapman et al. 2002c; Struhsaker 2008; Strier 2010). For example, both multi-male and uni-male social structures are documented for a number of species, and examples include black howler monkeys (*Alouatta pigra*—van Belle and Estrada 2006), red howlers (*Alouatta seniculus*—Pope 1991), and mountain gorillas (*Gorilla beringei*—Robbins 2001). This may result from the effect of the ecological differences between sites, demographic factors

like group size, or the effects of population density relative to carrying capacity (Pope 1991). Furthermore, ecological factors that influence diet and thereby likely social organization have been shown to be remarkably variable. For example, based on a study of 11 different groups of redtail monkeys (*Cercopithecus ascanius*), the proportion of time spent eating different plant parts was shown to vary dramatically (leaves 7–74%, fruit 13–61%, and insects 1–16%—Chapman et al. 2002b; see also the long-term research by Cords 1986, 1987). Similarly, while seasonal variation in diet has been appreciated for some time (Chapman 1987; Wright 1999; Lambert 2002), recent long-term studies are demonstrating strong interannual differences in the composition of a group's diet (Altmann 1998; Chapman et al. 2002c). Given that changes in diet are predicted to influence social organization, the effect of dietary variation warrants closer examination.

It is not just long-term variation in ecological variables that creates variation in social organization, long-term changes in social and demographic factors also influence social organization. For example, short-term studies may yield correlations between variables relevant to fitness, but such studies do not demonstrate whether the correlations remain over the long term. The classic example concerns the observation that dominance is generally positively correlated with instantaneous measures of reproductive success in many taxa, including many simians. However, do these snapshots accurately depict lifetime reproductive success, especially among species where tenure of alpha male status may be short lived? It may be that longevity is more important than dominance over the long term. For example, with male sifakas (*Propithecus verreauxi*) at the Beza Mahafaly Reserve in Madagascar, annual reproductive success has a strong influence on lifetime reproductive success; however, lifespan also has an important effect (Sussman et al. 2012).

Fitness can also be dramatically affected by rare and unpredictable events, which require long-term data to evaluate. A classic example features the importance of predation. For example, Isbell (1990) documented a sudden dramatic increase in mortality of vervet monkeys (*Cercopithecus aethiops*, also referred to *Chlorocebus aethiops*), which was thought to be due to predation from a leopard moving into the area. Long-lived species may also face sporadic and rare ecological crises. For example, prolonged drought or hurricanes can change which types of animals (e.g., male or female; dominant or subordinate) survive and reproduce, thus influencing social organization (Dittus 1985; Pavelka and Behie 2005).

Long-term research of primates has also allowed the recognition of the importance of kinship to elements such as dispersal and vocalization. For example, sex-biased dispersal typically is thought to reduce kin cooperation in the dispersing sex and thus represents a cost of dispersal to the sex moving to new groups (Isbell and Van Vuren 2014). Research involving long-term monitoring of multiple groups has documented that kinship may play a more important role than previously appreciated as dispersal among groups can involve either kin dispersing together or a dispersing animal moving into a group that already has kin (parallel dispersal—Schoof et al. 2009). For example, Jack

and colleagues (2014) collected demographic and genetic data from 2 to 5 groups of *Cebus capucinus* and documented that the majority of males dispersed in parallel. Findings such as this are only possible if long-term data are available. Similarly, Cheney and Seyfarth (1980, 1981, 1985) reported that vervet monkeys emit alarm calls and respond not only to the alarm call of others in a manner that demonstrates clear kinship bias, but that unrelated females look toward the mother of the infant in response to the playback of an infant's distress call. This illustrates the recognition of kinship and a high level of cognitive ability. There are a great number of studies that use long-term, site-specific data to evaluate the selective pressures and advantages of specific social organizations of behaviors, although it is not possible to review them all here (Altmann and Alberts 2005; Ostner et al. 2008; Schülke et al. 2010; Alberts and Altmann 2012; Fedigan and Jack 2012; Perry 2012, 2014; Perry et al. 2012).

POPULATION AND COMMUNITY ECOLOGY

Simians primarily influence the structure and the nature of community-level interactions through 3 mechanisms: seed dispersal and forest regeneration, the resulting mortality of preferred food trees, and competition with other species filling similar niches. Early studies of tropical fauna recognized that simians constitute a large proportion of the frugivore biomass (Eisenberg and Thorington 1973), they eat large quantities of fruit, and they defecate or spit out large numbers of undamaged seeds (Lieberman et al. 1979; Estrada and Coates-Estrada 1984; Corlett and Lucas 1990). For example, in Kibale National Park, Uganda, 98.5% of chimpanzee dung samples contain seeds, with an average of 22 seeds (> 2 mm) per defecation (Wrangham et al. 1994), such that chimpanzees disperse at least 369 large seeds km^{-2} day^{-1}. Frugivorous redtail monkeys, blue monkeys (*Cercopithecus mitis*), and mangabeys (*Lophocebus albigena*) in Kibale disperse 446 seeds km^{-2} day^{-1} (Lambert 1997). Similarly, the simian community of northern Costa Rica (*Ateles geoffroyi*, *Alouatta palliata*, *Cebus capucinus*) disperses 5,600 large seeds km^{-2} day^{-1} (Chapman 1989). These studies illustrate that simians are dispersing many seeds daily, and it has been demonstrated that these seeds are viable (Lieberman et al. 1979; Wrangham et al. 1994). This indicates that simians play an important role in structuring the future composition of forests.

This supposition is supported by other roles that simians play. Some simian species are influential in modifying the physical environment by changing, maintaining, or creating new habitats and some researchers have called them ecosystem engineers (Chapman et al. 2013a). Frugivorous simians likely do this through seed dispersal, but folivorous simians play a similarly important role in their abilities to kill trees through their foraging, stop fruit set through foraging on flowers, and slowing tree growth through excessive foraging on leaves (Chapman et al. 2013a). For example, using 14 years of data on feeding of red colobus (*Procolobus rufomitratus*, also referred to *Piliocolobus rufomitratus*), it was discovered that the flower crops of the forest tree *Markhamia lutea* were almost totally consumed by

monkeys every year, such that there was no subsequent fruit production (Chapman et al. 2013b). Correspondingly, 21 years of tree recruitment illustrated a general decline in its abundance across all size classes. Additionally, unlike most other mammals, apes can make tools that alter the environment (e.g., crack nuts and kill seeds); large differences in the culture of tool use can potentially create heterogeneity in the forest.

CONSERVATION

Worldwide, nearly 50% of simian species are at risk of extinction (Mittermeier et al. 2009, Estrada 2013), and 11% are classified as critically endangered by the International Union for Conservation of Nature (2014). Since simians are long lived, it can take a decade or more to quantify their response to anthropogenic changes to their ecosystem (Struhsaker 1973). Despite numerous threats to simian populations, one of the most important is habitat loss. In tropical countries, agricultural land usage increased by 48,000 km^2/year between 1999 and 2008 (Phalan et al. 2013), and global forest loss was estimated at 2.3 million km^2 between 2000 and 2012 (Hansen et al. 2013). Given the predicted increase in human population size and consequent higher consumption rates, it is expected that by 2050, the conversion of an additional ~1 billion ha of land—primarily in developing countries—will be necessary to meet increasing human consumption (Laurance et al. 2014). Unfortunately, the 3 regions where simians are found have a much higher human population growth rate than European countries (2.7%/year compared to 0.2%/year, respectively—Estrada 2013).

An example of habitat loss caused by anthropogenic changes was observed in Uganda. In 1995, Chapman and colleagues (2013c) surveyed the simian populations in 20 forest fragments (size from 0.8 to 130 ha) and confirmed the presence of permanent nonhuman primate residents or transient individuals in all fragments. Fifteen years later, only 3 of these fragments remained, most of the others having been cleared for fuelwood or timber (Naughton-Treves and Chapman 2002).

Another important threat to simians is climate change. Over the last 100 years, the global temperature has risen by approximately 0.6°C. Estimates by the Intergovernmental Panel on Climate Change (IPCC) suggest that warming could continue and, by the end of the century, the world could be 0.3–6.4°C warmer than it is today (Intergovernmental Panel on Climate Change 2007). Responses to climate change or anthropogenic damage like logging do not typically occur over the duration of a Ph.D. research project or granting cycle (1–3 years). Accurately documenting the change in tree and simian communities takes decades of detailed research. For example, it took 15–30 years for researchers in Kibale to demonstrate that leaf nutrient quality for folivorous monkeys was declining as predicted by greenhouse experiments mimicking climate change (Rothman et al. 2015). This again underlines the need for long-term research.

All forests occupied by simians are likely changing, either representing succession resulting from some previous anthropogenic disturbance or as a result of climate change. Since the mid-1980s, there has been an accumulation of evidence that many forests that were traditionally considered "old growth" or "pristine" forests have been disturbed relatively recently (i.e., recently in terms of the speed of forest regeneration, which is 200–4,000 years—Clark 1996). For example, the 1st paleoecological studies from the Darien of Panama, an area previously described as one of the last untouched Neotropical forests, revealed a 4,000-year-old history of human disturbance (Bush and Colinvaux 1994). Similar evidence has accumulated for other regions, particularly from Africa, Central America, and Amazonia (Gomez-Pompa 1987; Tutin and Oslisly 1995; Bush et al. 2007).

FUTURE DIRECTIONS

Given the conservation threats to primates, there is a clear need for long-term future research addressing conservation priorities. However, for academics and many practitioners this should not simply mean identifying a threat and paying lip service to a simple, and often obvious, solution (e.g., saying that to protect primates, stop bushmeat hunting or logging). Rather, they should be attempting to identify unexpected and often cascading effects of change that may be deleterious and will likely only be apparent by long-term monitoring. An example presented above is how climate change affects the nutritional value of foods of colobus monkeys (Rothman et al. 2015). We must be able to identify a conservation problem and understand its immediate and cascading consequences, since with this knowledge we can predict future change and thus construct informed conservation and management plans to prevent negative change from occurring. In addition, it is valuable to predict how interventions may promote positive change for primate populations. While the extent of deforestation is widely reported, the amount of land that is abandoned and regenerating to forest and the consequences of active reforestation on primate populations is poorly known. In the 1990s, it was estimated that secondary forests replaced at least 1 of every 6 ha of primary forest that was deforested and that secondary forests now represent 35% of all remaining tropical forests (Wright and Muller-Landau 2006). This is driven, in part, by the movement patterns of people—as of 2008, more people lived in cities than in rural settings (Wright and Muller-Landau 2006; Jacob et al. 2008). This urbanization trend is increasing and the United Nations Population Division estimates 90% of the world's population growth between 2000 and 2030 will occur in cities of the developing world (United Nations Population Division 2008). This movement of people from a rural to urban setting and efforts to restore tropical forests as part of carbon offset programs offers great conservation opportunities. However, little long-term data exist for such environments (but see Omeja et al., in press).

There is still a great deal to learn about many issues, some of which are: What are the cognitive abilities of primates? What are their nutritional strategies? How do they physiologically handle the range of habitats they occur in (e.g., from freezing cold to extreme heat, or from high elevation to sea level), and how flexible are different species in behavior and social organization and

how does this help each species handle anthropogenic change? This names just a few (Setchell 2013). Furthermore, studies that investigate basic biological questions or develop new theory often reveal information that becomes applicable to conservation (e.g., island biogeography theory became the basis for studies on how animals survive in fragments). Also, from a practical perspective, studies of basic science are vital because the vast majority of primate research is funded by governmental granting agencies that focus on theory and rarely conservation work. These research projects facilitate conservation, however, by getting researchers into the field and helping them complete their training. During periods when government funding is low, and to facilitate long-term research that is hard to finance through academic pursuits, foundations play a particularly important role and they are vital in communicating results to the public. For example, the World Wildlife Fund for Nature has more than 5 million supporters (Rands et al. 2010) and National Geographic Society media are viewed by approximately 400 million people each month (J. Francis, National Geographic Society, pers. comm.).

It is clear that long-term research will help address both basic science questions and conservation issues. As a result, we strongly encourage the development of long-term research initiatives, encourage granting agencies and foundations to pay increasing attention to them, and encourage researchers as a community to initiate and continue long-term studies, particularly adopting studies that others have started.

Supplementary Data

Supplementary Data SD1.—Examples of long-term field studies of primates (non-prosimians) that illustrate important contributions that long-term research brings to the field of mammalogy and theoretical biology in general. This is NOT meant to be a comprehensive review and we apologize in advance to those important studies and researchers we have not mentioned here.

Acknowledgments

Literature Cited

Alberts, S. C., and J. Altmann. 2012. The Amboseli Baboon Research Project: 40 years of continuity and change. Pp. 261–288 in Long-term field studies of primates (P. Kappeler and D. P. Watts, eds.). Springer, Berlin, Germany.

Altmann, S. A. 1998. Foraging for survival: yearling baboons in Africa. University of Chicago Press, Chicago, Illinois.

Altmann, J., and S. C. Alberts. 2005. Growth rates in a wild primate population: ecological influences and maternal effects. Behavioral Ecology and Sociobiology 57:490–501.

Bronikowski, A. M., and J. Altmann. 1996. Foraging in a variable environment: weather patterns and behavioural ecology of baboons. Behavioral Ecology and Sociobiology 39:11–25.

Bush, M. B., and P. A. Colinvaux. 1994. Tropical forest disturbance: paleoecological records from Darien, Panama. Ecology 75:1761–1768.

Bush, M. B., et al. 2007. Holocene fire and occupation in Amazonia: records from two lake districts. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 362:209–218.

Butynski, T. M. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density sub-populations. Ecological Monographs 60:1–26.

Carnegie, S. D., L. M. Fedigan, and T. E. Ziegler. 2011. Social and environmental factors affecting fecal glucocorticoids in wild, female white-faced capuchins (*Cebus capucinus*). American Journal of Primatology 73:1–9.

Carpenter, C. R. 1964. A field study of the behavior and social relations of howling monkeys. Pp. 9–32 in Naturalistic behavior of nonhuman primates (C. R. Carpenter, ed.). Pennsylvania State University Press, State College.

Chapman, C. A. 1987. Flexibility in diets of three species of Costa Rican primates. Folia Primatologica 49:90–105.

Chapman, C. A. 1989. Primate seed dispersal: the fate of dispersed seeds. Biotropica 21:148–154.

Chapman, C. A., et al. 2013a. Primates as ecosystem engineers. International Journal of Primatology 34:1–14.

Chapman, C. A., T. R. Bonnell, R. Sengupta, T. L. Goldberg, and J. M. Rothman. 2013b. Is *Markhamia lutea*'s abundance determined by animal foraging? Forest Ecology and Management 308:62–66.

Chapman, C. A., and L. J. Chapman. 1990. Reproductive-biology of captive and free-ranging spider monkeys. Zoo Biology 9:1–9.

Chapman, C. A., and L. J. Chapman. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates 40:215–231.

Chapman, C. A., and L. J. Chapman. 2002. Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. Comparative Biochemistry and Physiology, A. Comparative Physiology 133:861–875.

Chapman, C. A., L. J. Chapman, K. A. Bjorndal, and D. A. Onderdonk. 2002a. Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. International Journal of Primatology 23:283–310.

Chapman, C. A., et al. 2002b. Variation in the diets of *Cercopithecus* species: differences within forests, among forests, and across species. Pp. 319–344 in The guenons: diversity and adaptation in African monkeys (M. Glenn and M. Cords, eds.). Plenum, New York.

Chapman, C. A., L. J. Chapman, and T. R. Gillespie. 2002c. Scale issues in the study of primate foraging: red colobus of Kibale National Park. American Journal of Physical Anthropology 117:349–363.

Chapman, C. A., L. J. Chapman, L. Naughton-Treves, M. J. Lawes, and L. R. McDowell. 2004. Predicting folivorous primate abundance: validation of a nutritional model. American Journal of Primatology 62:55–69.

Chapman, C. A., et al. 2013c. Going, going, gone: a 15-year history of the decline of primates in forest fragments near Kibale National Park, Uganda. Pp. 89–104 in Primates in fragments: complexity

and resilience (L. K. Marsh and C. A. Chapman, eds.). Springer, New York.

CHAPMAN, C. A., AND J. M. ROTHMAN. 2009. Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. Primates 50:12–22.

CHAPMAN, C. A., R. W. WRANGHAM, AND L. J. CHAPMAN. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behavioural Ecology and Sociobiology 36:59–70.

CHENEY, D. L., AND R. M. SEYFARTH. 1980. Vocal recognition in free-ranging vervet monkeys. Animal Behaviour 28:362–367.

CHENEY, D. L., AND R. M. SEYFARTH. 1981. Selective forces affecting the predator alarm calls of vervet monkeys. Behaviour 56:25–61.

CHENEY, D. L., AND R. M. SEYFARTH. 1985. Vervet monkey alarm calls: manipulation through shared information? Behaviour 94:150–166.

CLARK, D. B. 1996. Abolishing virginity. Journal of Tropical Ecology 12:735–739.

CORDS, M. 1986. Interspecific and intraspecific variations in the diet of two forest guenons, *Cercopithecus ascanius* and *C. mitis*. Journal of Animal Ecology 55:811–827.

CORDS, M. 1987. Forest guenons and patas monkeys: male-male competition in one-male groups. Pp. 98–111 in Primate societies (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. Wrangham, and T. T. Struhsaker, eds.). Chicago University Press, Chicago, Illinois.

CORLETT, R. T., AND P. W. LUCAS. 1990. Alternative seed-handling strategies in primates - seed spitting by long-tailed macaques (*Macaca fascicularis*). Oecologia 82:171–190.

DAVIES, A. G. 1994. Colobine populations. Pp. 285–310 in Colobine monkeys: their ecology, behaviour and evolution (A. G. Davies and J. F. Oates, eds.). Cambridge University Press, Cambridge, United Kingdom.

DITTUS, W. P. J. 1985. The influence of leaf-monkeys on their feeding trees in a cyclone-disturbed environment. Biotropica 17:100–106.

EISENBERG, J. F., N. A. MUCKENHIRN, AND R. RUDRAN. 1972. The relation between ecology and social structure in primates. Science 176:863–874.

EISENBERG, J. F., AND R. W. THORINGTON. 1973. A preliminary analysis of a neotropical mammal fauna. Biotropica 5:150–161.

ESTRADA, A. 2013. Socioeconomic context of primate conservation: population, poverty, global economic demands, and sustainable land use. American Journal of Primatology 75:30–45.

ESTRADA, A., AND R. COATES-ESTRADA. 1984. Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. American Journal of Primatology 6:77–91.

FASHING, P. J., E. DIERENFELD, AND C. B. MOWRY. 2007. Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of *Colobus guereza* in Kakamega Forest, Kenya. International Journal of Primatology 28:673–703.

FEDIGAN, L. M., AND K. M. JACK. 2012. Tracking monkeys in Santa Rosa: lessons from a regenerating tropical dry forest. Pp. 165–184 in Long-term field studies of primates (P. Kappeler and D. P. Watts, eds.). Springer Press, New York.

FERNANDEZ-DUQUE, E. 2007. Social monogamy in the only nocturnal haplorhines. Pp. 139–154 in Primates in perspective (C. Campbell, A. Fuentes, K. MacKinnon, S. Bearder, and R. Stumpf, eds.). Oxford University Press, Oxford, United Kingdom.

FERNANDEZ-DUQUE, E., A. DI FIORE, AND G. CARRILLO-BILBAO. 2008. Behavior, ecology, and demography of *Aotus vociferans* in Yasuní National Park, Ecuador. International Journal of Primatology 29:421–431.

FRANZ, M., J. ALTMANN, AND S. C. ALBERTS. 2015. Knockouts of high-ranking males have limited impact on baboon social networks. Current Biology 61:107–113.

GANZHORN, J. U. 2002. Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics. Oecologia 131:427–435.

GARTLAN, J. S., AND C. K. BRIAN. 1968. Ecology and social variability in *Cercopithecus aethiops* and *C. mitis*. Pp. 253–292 in Primates (P. Jay, ed.). Hold, Rinehard, and Winston, New York.

GESQUIERE, L. R., ET AL. 2005. Coming of age: steroid hormones of wild immature baboons (*Papio cynocephalus*). American Journal of Primatology 67:83–100.

GESQUIERE, L. R., ET AL. 2008. Coping with a challenging environment: effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons (*Papio cynocephalus*). Hormones and Behavior 54:410–416.

GESQUIERE, L. R., N. H. LEARN, M. C. M. SIMAO, P. O. ONYANGO, S. C. ALBERTS, AND J. ALTMANN. 2011. Life at the top: rank and stress in wild male baboon. Science 333:357–360.

GOMEZ-POMPA, A. 1987. On Maya silviculture. University of California Press, Berkeley.

HANSEN, M. C., ET AL. 2013. High-resolution global maps of 21st-century forest cover change. Science 342:850–853.

INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE (IPCC). 2007. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change, 2007. Cambridge University Press, Cambridge, United Kingdom.

INTERNATIONAL UNION FOR CONSERVATION OF NATURE (IUCN). 2014. IUCN Red List of Threatened Species. Version 2014.2. www.iucnredlist.org. Accessed 6 November 2014.

ISBELL, L. A. 1990. Sudden short-term increase in mortality in vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park, Kenya. American Journal of Primatology 21:41–52.

ISBELL, L. A. 1991. Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. Behavioral Ecology 2:143–155.

ISBELL, L. A., AND D. VAN VUREN. 2014. Differential costs of locational and social dispersal and their consequences for female group-living. Behaviour 133:1–36.

JACK, K. M., F. A. CAMPOS, L. M. FEDIGAN, AND A. SATO. 2014. The effect of male parallel dispersal on the kin composition of groups in white-faced capuchins. Animal Behaviour 96:9–17.

JACOB, A. L., I. VACCARO, R. SENGUPTA, J. HARTTER, AND C. A. CHAPMAN. 2008. How can conservation biology best prepare for declining rural population and ecological homogenization? Tropical Conservation Science 1:307–320.

JANSON, C. H., AND C. P. VAN SCHAIK. 1988. Recognizing the many faces of primate food competition: methods. Behaviour 105:165–186.

KAPPELER, P. M., L. BARRETT, D. T. BLUMSTEIN, AND T. H. CLUTTON-BROCK. 2013. Constraints and flexibility in mammalian social behaviour: introduction and synthesis. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 368:20120337.

KAPPELER, P. M., AND C. P. VAN SCHAIK. 2002. Evolution of primate social systems. International Journal of Primatology 23:707–740.

KNOTT, C. D. 1998. Changes in orangutan caloric intake, energy balance and ketones in response to fluctuating fruit availability. International Journal of Primatology 19:1061–1079.

KOENIG, A., AND C. BORRIES. 2006. The predictive power of socioecological models: a reconsideration of resource characteristics, agonism and dominance hierarchies. Pp. 263–284 in Feeding ecology in apes and other primates (G. Hohmann, M. M. Robbins, and C. Boesch, eds.). Cambridge University Press, Cambridge, United Kingdom.

LAMBERT, J. E. 1997. Fruit processing and seed dispersal by chimpanzees (*Pan troglodytes schweinfurthii*) and redtail monkeys (*Cercopithecus ascanius schmidti*) in the Kibale National Park, Uganda. University of Illinois, Urbana.

LAMBERT, J. E. 2002. Resource switching in guenons: a community analysis of dietary flexibility. Pp. 303–317 in The guenons: diversity and adaptation in African monkeys (M. Glenn and M. Cords, eds.). Kluwer Academic Press, New York.

LAURANCE, W. F., J. SAYER, AND K. G. CASSMAN. 2014. Agriculture expansion and its impacts on tropical nature. Trends in Ecology and Evolution 29:107–116.

LIEBERMAN, D., J. B. HALL, M. D. SWAINE, AND M. LIEBERMAN. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. Ecology 60:65–75.

MILTON, K., AND J. GIACALONE. 2014. Differential effects of unusual climatic stress on capuchin (*Cebus capucinus*) and howler monkey (*Alouatta palliata*) populations on Barro Colorado Island, Panama. American Journal of Primatology 76:249–261.

MILTON, K., J. GIACALONE, S. J. WRIGHT, AND G. STOCKMAYER. 2005. Do frugivore population fluctuations reflect fruit production? Evidence from Panama. Pp. 5–35 in Tropical fruits and frugivores (D. J. Lawrence and J. P. Boubli, eds.). Springer, New York.

MITTERMEIER, R. A., ET AL. 2009. Primates in peril: the world's 25 most endangered primates 2008–2010. Primate Conservation 24:1–57.

MULLER, M. N., AND R. W. WRANGHAM. 2004. Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). Behavioral Ecology and Sociobiology 55:332–340.

NAUGHTON-TREVES, L., AND C. A. CHAPMAN. 2002. Fuelwood resources and forest regeneration on fallow land in Uganda. Journal of Sustainable Forestry 14:19–32.

NICHOLSON, A. J. 1933. The balance of animal populations. Journal of Animal Ecology 2:132–178.

OATES, J. F., ET AL. 1990. Determinants of variation in tropical forest primate biomass: new evidence from West Africa. Ecology 71:328–343.

OMEJA, P. A., M. J. LAWES, A. CORRIVEAU, K. VALENTA, F. P. PAIM, AND C. A. CHAPMAN. In press. Recovery of the animal and plant communities across large scales in Kibale National Park, Uganda. Biotropica.

OSTNER, J., M. HEISTERMANN, AND O. SCHÜLKE. 2008. Dominance, aggression and physiological stress in wild male Assamese macaques (*Macaca assamensis*). Hormones and Behavior 54:613–619.

PAVELKA, M. S. M., AND A. M. BEHIE. 2005. The effect of Hurricane Iris on the food supply of black howlers (*Alouatta pigra*) in southern Belize. Biotropica 37:102–108.

PERRY, S. 2012. The behavior of wild white-faced capuchins: demography, life history, social relationships, and communication. Advances in the Study of Behaviour 44:135–181.

PERRY, S. E. 2014. The importance of long-term fieldwork for answering evolutionary questions: the Lomas Barbudal Monkey Project in Costa Rica as a case study. American Journal of Physical Anthropology 153:206–206.

PERRY, S., I. GODOY, AND W. LAMMERS. 2012. The Lomas Barbudal Monkey Project: two decades of research on *Cebus capucinus*. Pp. 141–163 in Long-term field studies of primates (P. M. Kappeler and D. P. Watts, eds.). Springer, New York.

PHALAN, B., ET AL. 2013. Crop expansion and conservation priorities in tropical countries. PLoS One 8:e51759.

POPE, T. R. 1991. Effects of demographic change on group kin structure and gene dynamics of populations of red howling monkeys. Journal of Mammalogy 79:692–712.

RANDS, M. R. W., ET AL. 2010. Biodiversity conservation: challenges beyond 2010. Science 329:1298–1303.

ROBBINS, M. M. 2001. A demographic analysis of male life history and social structure of mountain gorillas. Behaviour 131:21–47.

ROTHMAN, J. M., C. A. CHAPMAN, T. T. STRUHSAKER, D. RAUBENHEIMER, D. TWINOMUGISHA, AND P. G. WATERMAN. 2015. Cascading effects of global change: decline in nutritional quality of tropical leaves. Ecology 96:873–878.

SAJ, T. L., S. MARTEINSON, C. A. CHAPMAN, AND P. SICOTTE. 2007. Controversy over the application of current socioecological model to folivorous primates: *Colobus vellerosus* fits the predictions. American Journal of Physical Anthropology 133:994–1003.

SCHOOF, V. A. M., T. B. BONNELL, K. M. JACK, T. E. ZIEGLER, A. D. MELIN, AND L. M. FEDIGAN. 2016. Male endocrine response to seasonally varying environmental and social factors in a Neotropical primate, *Cebus capucinus*. American Journal of Physical Anthropology 159:671–682.

SCHOOF, V. A., K. M. JACK, AND L. A. ISBELL. 2009. What traits promote male parallel dispersal in primates? Behaviour 146:701–726.

SCHOOF, V. A. M., K. M. JACK, AND T. E. ZIEGLER. 2014. Male response to female ovulation in white-faced capuchins (*Cebus capucinus*): variation in testosterone, DHT, and glucocorticoid production. International Journal of Primatology 35:643–660.

SCHÜLKE, O., J. BHAGAVATULA, L. VIGILANT, AND J. OSTNER. 2010. Social bonds enhance reproductive success in male macaques. Current Biology 20:2207–2210.

SETCHELL, J. M. 2013. Top 10 questions in primatology. International Journal of Primatology 34:647–661.

SNAITH, T. V., AND C. A. CHAPMAN. 2005. Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus. Behavioral Ecology and Sociobiology 59:185–190.

SNAITH, T. V., AND C. A. CHAPMAN. 2007. Primate group size and socioecological models: do folivores really play by different rules? Evolutionary Anthropology 16:94–106.

SNAITH, T. V., AND C. A. CHAPMAN. 2008. Red colobus monkeys display alternative behavioural responses to the costs of scramble competition. Behavioural Ecology 19 1289–1296.

STERCK, E. H. M., D. P. WATTS, AND C. P. VAN SCHAIK. 1997. The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41:291–309.

STRIER, K. B. 2010. Long-term field studies: positive impacts and unintended consequences. American Journal of Primatology 72:772–778.

STRUHSAKER, T. T. 1973. A recensus of vervet monkeys in the Masai-Amboseli Game Reserve, Kenya. Ecology 54:930–932.

STRUHSAKER, T. T. 2008. Demographic variability in monkeys: implication for theory and conservation. International Journal of Primatology 28:19–34.

STRUHSAKER, T. T., AND L. LELAND. 1979. Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. Advances in the Study of Behavior 9:159–228.

SUSSMAN, R. W., ET AL. 2012. Beza Mahafaly Special Reserve: long-term research on lemurs in Southwestern Madagascar. Pp. 45–66 in Long-term field studies of primates (P. M. Kappeler and D. P. Watts, eds.). Springer, Heidelberg, Germany.

TERBORGH, J. 1983. Five new world primates. Princeton University Press, Princeton, New Jersey.

TUTIN, C. E. G., AND R. OSLISLY. 1995. *Homo, Pan*, and *Gorilla*: coexistence over 60,000 years at Lope in central Gabon. Journal of Human Evolution 28:597–602.

UNITED NATIONS POPULATION DIVISION. 2008. World urbanization prospects: the 2007 revision. http://esa.un.org/unup/index.asp?panel=1. Accessed 23 February 2008.

VAN BELLE, S., AND A. ESTRADA. 2006. Demographic features of *Alouatta pigra* populations in extensive and fragmented forests. Pp. 121–142 in New perspectives in the study of Mesoamerican primates (A. Estrada, P. A. Garber, M. S. M. Pavelka, and L. Luecke, eds.). Springer, New York.

VAN SCHAIK, C. P. 1989. The ecology of social relationships amongst female primates. Pp. 195–218 in Comparative socioecology: the behavioural ecology of humans and other mammals (V. Standen and R. A. Foley, eds.). Blackwell Scientific Publications, Boston, Massachusetts.

WATERMAN, P. G., J. A. M. ROSS, E. L. BENNET, AND A. G. DAVIES. 1988. A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. Biological Journal of the Linnean Society 34:1–32.

WRANGHAM, R. W. 1980. An ecological model of female-bonded primate groups. Behaviour 75:262–300.

WRANGHAM, R. W., C. A. CHAPMAN, AND L. J. CHAPMAN. 1994. Seed dispersal by forest chimpanzees In Uganda. Journal of Tropical Ecology 10:355–368.

WRIGHT, P. C. 1999. Lemur traits and Madagascar ecology: coping with an island environment. Yearbook of Physical Anthropology 43:31–72.

WRIGHT, S. J., AND H. C. MULLER-LANDAU. 2006. The future of tropical forest species. Biotropica 38:287–301.

Special Feature Editor was Barbara H. Blake.