



Annual Review of Anthropology

Effects of Environmental Stress on Primate Populations

Jason M. Kamilar¹ and Lydia Beaudrot²

¹Department of Anthropology and Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, Massachusetts 01002, USA; email: jkamiliar@umass.edu

²Department of Ecology and Evolutionary Biology, and Michigan Society of Fellows, University of Michigan, Ann Arbor, Michigan 48109, USA; email: beaudrot@umich.edu

Annu. Rev. Anthropol. 2018. 47:417–34

The *Annual Review of Anthropology* is online at anthro.annualreviews.org

<https://doi.org/10.1146/annurev-anthro-102317-045949>

Copyright © 2018 by Annual Reviews.
All rights reserved

Keywords

climate variability, human impacts, monitoring, population ecology, predation, resource availability

Abstract

Environmental stress on primate populations can take many forms. Abiotic factors, such as temperature and precipitation, may directly influence the behavior of primates owing to physiological demands of thermoregulation or through indirect influences on vegetation that primates rely on for food. These effects can also scale up to the macro scale, impacting primate distributions and evolution. Primates also encounter stress during interactions within and between species (i.e., biotic interactions). For example, selective pressure from male-perpetrated infanticide can drive the development of female counterstrategies and can impact life-history traits. Predation on primates can modify group size, ranging behavior, and habitat use. Finally, humans have influenced primate populations for millennia. More recently, hunting, habitat disturbance, disease, and climate change have increased in frequency and severity with detrimental impacts on primate populations worldwide. These effects and recent evidence from camera traps emphasize the importance of maintaining protected areas for conserving primate populations.

INTRODUCTION

Environmental stress refers to a condition that affects the performance and well-being of an organism (Bijlsma & Loeschcke 2005). Its effects can occur at a range of scales from the molecular (e.g., glucocorticoid production) to the population level (e.g., change in abundance, age structure) and beyond (Cairns 2013). The definition of what constitutes an environmental stress inherently depends on the organism of interest because what is stressful for one species may not cause stress for another (e.g., drought conditions are more stressful for non-desert-adapted species). Ultimately, environmental stress can reduce reproductive fitness, which in turn has consequences for population dynamics. Environmental stress can thereby drive adaptations over evolutionary time.

There are three broadscale types of environmental stress. The first is abiotic stress, which results from nonliving aspects of the environment, such as temperature and precipitation. Abiotic stress is expected to be lowest for species when they occur in the environmental conditions to which they are best adapted, and stress is likely to increase as species experience abiotic conditions outside the range of conditions to which they are best adapted. Changes in abiotic conditions likely impact cold-blooded organisms more than warm-blooded animals (Buckley et al. 2012). However, many tropical organisms have narrower thermal tolerances than do temperate organisms because climate varies less in the tropics than it does further from the equator (Deutsch et al. 2008, Janzen 1967, Khaliq et al. 2014). Abiotic conditions may consequently affect primates more strongly than other mammalian orders because primates are an essentially tropical order. Abiotic stressors ultimately set the geographic limits of primate distributions.

The second type of environmental stress is biotic stress, which is stress due to interactions within species or between species. Like all organisms, biotic interactions can cause stress for primates. Several aspects of primate behavioral ecology, such as intergroup aggression and infanticide, cause stress when wounding and death occur. Stress from competition with conspecifics becomes increasingly important for primates when overpopulation occurs. Primate populations can be regulated by the availability of food during times of scarcity as well as by predation.

Third, human impacts from habitat loss, hunting, and climate change result in anthropogenic stress on populations. Both hunting and habitat loss are major threats that affect numerous primate populations worldwide. Climate change is an emergent threat whose effects have received relatively little investigation in the primate literature. Sources of abiotic, biotic, and anthropogenic environmental stress rarely operate in isolation and can have synergistic effects.

Finally, we highlight a recent biodiversity assessment from a global camera trap monitoring network, the Tropical Ecology Assessment and Monitoring (TEAM) Network. TEAM uses a standardized data collection protocol in tropical forest protected areas around the world. We examine the status of 24 Old World primate populations that TEAM monitors and consider them in relation to potential anthropogenic stressors, including hunting and habitat fragmentation. The TEAM data suggest that protected areas are an important conservation tool for supporting stable populations of primates.

ABIOTIC STRESS

Although primates are largely a tropical Order, there is significant variation in the abiotic conditions that populations experience. Therefore, there is a rich history of research examining how primates respond to abiotic factors. In fact, an abundant literature has addressed the relationship between climatic variables, such as temperature and rainfall, and a variety of primate traits, including behavior (Bronikowski & Altmann 1996, Dunham et al. 2011, Kamilar & Baden 2014, Kamilar & Marshack 2012), morphology (e.g., Cardini et al. 2007, Gordon et al. 2013, Jablonski & Chaplin 2010, Kamilar et al. 2012, Kamilar & Bradley 2011) and life history (Dewar & Richard

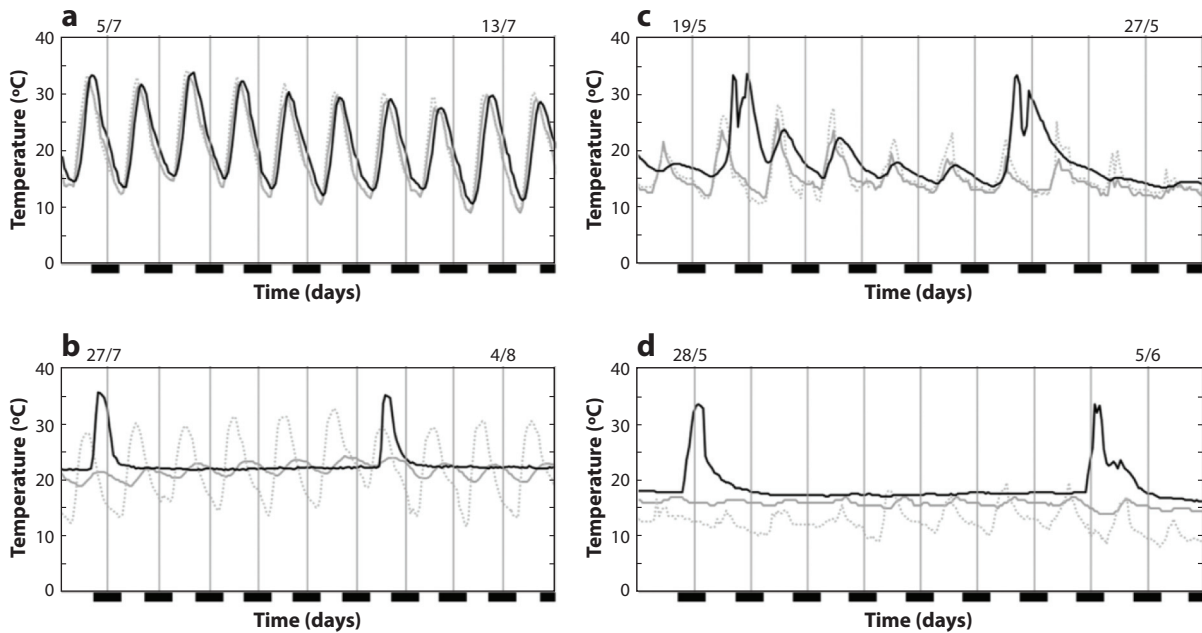


Figure 1

Example of the impact of cold temperature on western and fat-tailed dwarf lemurs. Temperature profiles for *Cheirogaleus medius* (a,b) and *C. crossleyi* (c,d) occupying poorly insulated (a,c) or highly insulated (b,d) hibernacula. For *C. medius*: skin (solid black), tree hole (solid gray), and ambient (dotted) temperatures; for *C. crossleyi*: skin (solid black), nest or underground (solid gray), and ambient (dotted) temperatures. Vertical lines indicate midnight; black bars indicate dark phase. Figure and figure legend text adapted from Blanco et al. (2013).

2007). Abiotic factors may directly influence primate traits or they may serve as an intermediary by influencing biome-scale vegetation patterns, which in turn drive variation in primate biology. In many cases, the specific mechanisms leading to phenotypic variation are difficult to discern. Although adaptation is often inferred, other processes such as plasticity may be important to consider (Strier 2017, West-Eberhard 2003).

Abiotic Stress at the Behavioral Level

At the level of behavioral ecology, many primatologists have investigated seasonal changes in temperature and/or rainfall in relation to food availability and distribution and how these factors influence various aspects of primate behavior, such as diet, activity budgets, ranging patterns, and mating behavior (for examples, see Brockman & van Schaik 2005, Lewis & Kappeler 2005, Strier et al. 1999). One of the more surprising and extreme relationships between temperature and primate behavior was recently discovered by Blanco and colleagues (2013) (**Figure 1**). They found that two dwarf lemur species (*Cheirogaleus sibreei* and *C. crossleyi*) in Eastern Madagascar hibernated underground for long periods of time. Specifically, this research was conducted at Tsinjoarivo, a high-altitude rainforest that is one of the colder locations in Madagascar. During their study period, the researchers documented a maximum ambient temperature of 22°C and a minimum value of 5°C. The lemurs' body temperatures matched that of the surrounding soil (~15°C) for more than 10 days at a time, and the total duration of their hibernation period was 3–6 months. This measurement is more than 15°C lower than their typical body temperature when

they are active. Although energetic data were unavailable, presumably these species save a substantial amount of energy during this period that would otherwise be used during thermoregulation. In addition, considering the body mass of the dwarf lemurs (250–350 g) and the near freezing ambient temperatures, hibernating in a 15°C microenvironment may prevent hypothermia.

In addition to seasonal shifts, interannual variation in climate may also have important impacts on primate populations. Campos and colleagues (2017) harnessed multiyear (17.6 to 51.9 years) survival rate, fertility rate, and climate data for 7 primate species. They found that climate variability did not correspond to survival rates for nearly all species and age classes, with the lone exception of infant sifakas (*Propithecus verreauxi*). More rainfall during the birth season (which is also the dry season) was related to increased infant survival. The lack of climate effects on survival rates for the other species/age classes may be a true effect but may also be related to relatively small sample sizes. Relatively small effects on species survival could have significant consequences on primate populations over longer time scales. In contrast with survival rates, climate variables did have a noticeable impact on the female fertility of three primate species: sifaka, blue monkey (*Cercopithecus mitis*), and northern muriqui (*Brachyteles hypoxanthus*). The variables and direction of climate variables differed across species. Warmer and wetter conditions were associated with increased sifaka fertility. Cooler temperatures and increased rainfall corresponded to higher blue monkey fertility. Cooler temperatures, but no rainfall effect, were associated with increased muriqui fertility. As Campos and colleagues (2017) note, the three species most affected by climate exhibit the highest levels of breeding seasonality of all taxa included in their study. This finding may have significant implications for predicting which species will be most impacted by future climate change.

Abiotic Stress at the Macro Level

Other studies have examined the relationship between abiotic factors and primate ecology at the community level (Beaudrot & Marshall 2011, Kamilar 2009, Reed & Fleagle 1995, Rowan et al. 2016). This scale of analysis exhibits emergent properties from the composite populations and species (Kamilar & Beaudrot 2013). For example, the tropical forests of the world contain the highest levels of primate biodiversity as compared to other types of environments (Fleagle 2013, Myers et al. 2000). Tropical rainforest areas are associated with high annual rainfall, warm temperatures, and relatively little seasonality in these abiotic variables. The connection between climate and primate biodiversity is mediated, at least in part, by vegetation (Kay et al. 1997). Regions of high plant productivity contain many primate species. Rainforests and their complex habitat structure support primate species that occupy a wide variety of ecological niches. Kamilar (2009) found that continent-wide variation in rainfall and temperature is associated with the species composition of primate communities in Africa, Madagascar, and the Neotropics. For example, guenons (*Cercopithecus* spp.) are more likely to be found at African study sites with high rainfall, whereas baboons (*Papio* sp.) are more likely to be found in a community associated with low rainfall. These results illustrate that some primate species are adapted to particular niches found in certain habitats.

More recently, new analytical tools and data availability have allowed researchers to ask new questions or address old questions in new ways. These new approaches include species distribution modeling (i.e., ecological niche modeling), which seeks to understand species geographic ranges as a function of environmental factors. Most commonly, abiotic variables are used to predict the areas that have suitable conditions for a species, with the assumption that the abiotic conditions where a species currently occurs determine where it will be able to persist (Araujo & Peterson 2012). These models can be used to investigate questions related to conservation biology, speciation, and taxonomy (Blair et al. 2013, Raxworthy et al. 2007, Thorn et al. 2009). For example, Kamilar

and colleagues (2016) quantified the known climatic niches of six mouse lemur species (*Microcebus* spp.) to investigate the degree of niche overlap among taxa. They found that these mouse lemur species exhibited significantly different climate niches from each other. These results support the idea that climate plays an important role in the distribution of these species. Also, if climatic niche is an indicator of species delineation, then these findings provide additional evidence that the six mouse lemur taxa should be treated as separate species.

At deep time scales, abiotic stressors can drive adaptation, speciation, and extinction (Lehman & Fleagle 2006). Changing climates can result in habitat modification, and existing species living in these habitats may be unable to disperse to more suitable areas. Therefore, some species may become extinct, while others may evolve traits to survive in the new environment (Ganzhorn et al. 2003). Species may also exhibit disjunct populations owing to the disappearance of the required habitat throughout their geographic range. These isolated populations may evolve traits that eventually lead to the formation of new species (Kamilar et al. 2009). This process may be especially relevant for forest-adapted species with limited dispersal ability, such as many primates (Beaudrot et al. 2014). Small- to medium-sized arboreal mammals are often unable to disperse across large areas of deforested habitat. The primates with these ecological characteristics may be most at risk of extinction or speciation if their population size is stable.

BIOTIC STRESS

Multiple types of interactions within and between species can negatively affect primates with consequences at the population level. For example, intergroup aggression and infanticide can decrease the abundance of a population. Competition between individuals of a species over available resources can result in poor body condition and ultimately negative population growth, and predation results in the death of primate prey. Different types of biotic stress typically impact life-history stages in different ways. Adult males are more likely to be injured during intergroup aggression, infants are killed through infanticide, and adult females experience disproportional stress from infanticide and low resource availability.

Intergroup Aggression

Intergroup aggression within primates is highly variable between species and can vary between multiple populations of a single species. Crofoot & Wrangham (2010) suggest that conflict between groups of primates is broadly used to maintain access to resources for long-term fitness despite this range of variation. At the aggressive end of the spectrum, both chimpanzees (*Pan troglodytes*) and white-faced capuchins (*Cebus capucinus*) engage in violent coalitionary attacks that can result in the injury or death of participants (Gros-Louis et al. 2003, Wilson et al. 2014). Lethal aggression has also been observed in spider monkeys (*Ateles geoffroyi*) (Campbell 2006, Valero et al. 2006) and white-handed gibbons (*Hylobates lar*) (Palombit 1993). In these extreme cases, the net effect of intergroup aggression is a decline in the abundance of individuals in a population and a change in the age structure of the populations. Most often, lethal aggression disproportionately affects adult males.

Infanticide

Infanticide, or the killing of an infant, is widespread across invertebrates and vertebrates. Animals commit infanticide for a variety of reasons: to obtain a food source, to reduce competition for food or space, to avoid providing parental care to unrelated offspring (e.g., in birds), or as a male reproductive strategy (Ebensperger 1998). Within primates, infanticide occurs in strepsirhines,

monkeys, and apes. The net effects of infanticide are a decline in reproductive success for the adult female whose offspring has been lost, a reduction in the number of individuals at the population level, and a change in the age structure of the population. Thus, infanticide disproportionately stresses infants and reproductive females. Selective pressure from infanticide can drive the development of counterstrategies, anti-infanticidal adaptations, and life-history evolution. For example, female Bornean orangutans (*Pongo pygmaeus*) mate with nonprime males when conception risk is low as an anti-infanticidal counterstrategy to confuse paternity (Crowley et al. 2009). Gelada females (*Theropithecus gelada*) have been shown to abort fetuses following male takeovers, which is likely an adaptation that prevents females from continued investment in offspring that would suffer infanticide, known as the Bruce effect (Roberts et al. 2012). The coat color of ursine colobus infants (*Colobus vellerosus*) at high risk of infanticide transitions to adult color more rapidly than the coats of infants at low risk, which suggests that infanticide influences life-history characteristics in this species (Bădescu et al. 2016).

Resource Availability

When the size of a population exceeds the level of resources necessary to sustain it (i.e., carrying capacity), competition between individuals can cause population growth to decline. This concept is known as density dependence. Multiple examples of density dependence in primates have been documented. The free-ranging population of rhesus macaques (*Macaca mulatta*) on the island of Cayo Santiago provides an example of density dependence in primates: Fertility rates declined as the number of adult females increased (Hernández-Pacheco et al. 2013) (**Figure 2**). The presence of density dependence in this provisioned population where food is consistently available suggests that density dependence likely has a stronger influence on population dynamics in wild primates for whom resource fluctuations occur more frequently.

Resource availability may affect primate populations more significantly when periods of low food availability are either unpredictable or extreme. For example, the masting dipterocarp forests of Southeast Asia fruit in irregular boom-and-bust cycles that can span nearly a decade (Cannon et al. 2007). In the case of the Bornean orangutan (*Pongo pygmaeus*), times of food scarcity cause

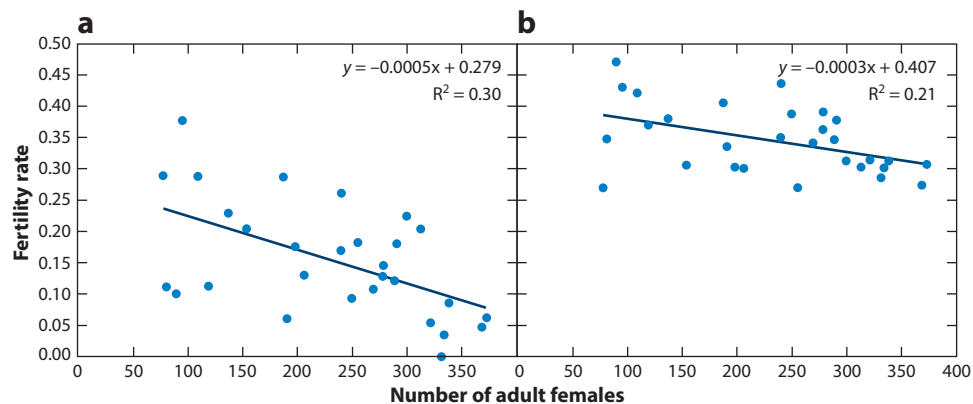


Figure 2

Example of density dependence in rhesus macaques on Cayo Santiago. Linear relationship between fertility rate of young adults (a) and adults (b) and the number of adult females. Figure adapted from Hernández-Pacheco et al. (2013).

energetic stress, which is indicated by the levels of ketones or C-peptide in orangutan urine (Knott 1998, Thompson & Knott 2008). These extended periods of food scarcity may have contributed to the prolonged interbirth interval in this species, thus influencing life-history evolution. Also in Borneo, variation in the amount of food available—particularly the density of figs—drives variation across habitats in the population density of white-bearded gibbons (*Hylobates albibarbis*) (Marshall & Leighton 2006). This relationship suggests that resource availability is a major determinant of population regulation in this species. Furthermore, the local abundance of pig-tailed macaques (*Macaca nemestrina*) in forests throughout Borneo does not vary with clouded leopard (*Neofelis diardi*) abundance, which suggests that resource availability rather than predation likely limits the population density of this species (Brodie & Giordano 2013).

For other species in other regions of the world, the extent to which resource availability limits population growth may depend on predator abundances. For example, Terborgh et al. (2001) describe a natural experiment in which a dammed river in Venezuela created a large lake. Islands from the emergent mountaintops were the only habitat that remained; no predators occurred on the islands. In the following decade, the density of howler monkeys (*Alouatta seniculus*) skyrocketed, and ultimately reproductive suppression occurred. This occurrence suggests that competition for available resources limited howler monkey population growth on the islands via increased stress on reproductive females, but only due to the absence of predators.

Predation

The cost of predation is particularly high for primates because of their long life spans and slow life histories. Arboreality and group living likely evolved in primates as antipredator defenses. For example, white-faced capuchins perceive greater danger near the ground and reduced predation risk in the middle and high layers of the forest canopy (Campos & Fedigan 2014). Group living simultaneously increases vigilance and decreases the likelihood of predation on any given group member. Indeed, predators favor terrestrial prey and small group sizes (Arlet & Isbell 2009, Shultz & Finlayson 2010).

As a consequence of the high costs of predation for primates, predation risk alone has measurable consequences. For example, perceived risk can influence ranging behavior in vervets more so than does resource availability (Willems & Hill 2009). This behavior seems particularly reasonable when considering that, between 1985 and 1987, leopards annually consumed between 5% and 70% of the vervet population in Amboseli National Park (Isbell 1990). While the major predators of primates include snakes, raptors, and terrestrial carnivores, the level of stress that each predatory species causes depends on the identity of the prey species. For example, vervets avoid areas used by leopards and chacma baboons more than areas used by snakes and eagles (Willems & Hill 2009), whereas male gray-cheeked mangabeys who chased away eagles exhibited elevated stress hormones (Arlet & Isbell 2009). In a unique example with one primate species hunting another, chimpanzees have driven a long-term decline in red colobus at Ngogo (Watts & Amsler 2013). The extent to which the red colobus population will be able to recover remains unclear, thus the consequences of predation for this primate population have been grave.

ANTHROPOGENIC STRESS

Hunting

Humans have co-occurred with nonhuman primates since the origin of the *Homo* lineage. Early humans hunted and/or scavenged a wide variety of mammal species, and primates are probably no exception to this pattern. Many modern human hunter-gatherers hunt primates as a necessary

protein source. Traditional hunting methods (using nets, darts, arrows, etc.) may have had an impact on many primate populations, potentially resulting in altered distributions and/or extinctions on a broad scale. For example, mounting evidence has indicated that large Malagasy primate extinctions in the last few thousand years are due primarily to hunting by humans (Crowley et al. 2017, Godfrey & Irwin 2007). Similarly, evidence shows that humans contributed to the Pleistocene extinctions of orangutans on mainland Southeast Asia and Java (Harrison et al. 2006).

The adoption of modern hunting techniques, such as guns, have changed historic dynamics, resulting in widespread population declines in many parts of the world (Fa et al. 2000, Linder & Oates 2011, Peterson 2003). Peres (1990) compared primate populations in western Amazonia sites that experienced hunting by humans versus those that were undisturbed. He showed that pressure from hunting by humans resulted in lower abundance levels for the largest Neotropical primates at these sites, the atelines. Large arboreal primates appear to be the species hunted most by humans in these areas, which has serious implications for the long-term viability of these primates. In addition to experiencing higher hunting rates, these species exhibit slower life-history traits, which decreases their ability to maintain their population size. Reduced population sizes and recent extirpations of these primate species may also impact the broader primate community in the form of density compensation (MacArthur et al. 1972, Peres & Palacios 2007). Peres & Dolman (2000) found that sites with increased hunting pressure were associated with reduced primate biomass due to declines in large species. The biomass of medium-sized primates increased at hunted sites, but the biomass of small primates did not. Because overlapping niches are necessary for density compensation to occur, small primates could not take advantage of increased resources available in the environment due to the lower biomass of large species because these resources were not a component of their niche space (Chapman et al. 2013).

The reasons for hunting primates include crop raiding (Hill 2000, Strum 2010) and providing a high-quality food source for human populations, among other reasons. The increased occurrence of hunting for food may be due to increases in human population, poverty, and food insecurity (Borgerson et al. 2016). A study of orangutan hunting on Borneo found that most people who have killed orangutans did so for food and not because of conflict (Davis et al. 2013). The problem of highly impoverished people having few options to provide food for their families will not be solved anytime soon. Anthropologists may be in a unique position to play a positive role in addressing this challenge by providing critical insights into the cultural and nutritional requirements of people, as well as the nonhuman primates and other animals that coexist with them (Marshall & Wich 2016).

Habitat Loss and Fragmentation

In addition to hunting nonhuman primates, humans can also negatively impact primate populations through directly modifying natural habitats. Human population size is currently more than seven billion and is projected to increase to more than nine billion by 2050 (Lutz et al. 2017). Primates are found in many countries with high human population growth rates, and increasing human populations are associated with greater habitat loss and fragmentation (Estrada et al. 2017). Many primates are especially sensitive to anthropogenically modified habitats because these mammals are forest dependent. Forests are often clear-cut for agricultural land (e.g., oil palm plantations) or to harvest wood (Ancrenaz et al. 2015, Kamilar & Tecot 2016, Soares-Filho et al. 2006). A recent global meta-analysis comparing primate biodiversity metrics (e.g., species richness, diversity, abundance) in disturbed versus nearby relatively intact forest found that human impacts produced negative effects on primate populations (de Almeida-Rocha et al. 2017). Forest conversion for agricultural development had the most negative impact on primate biodiversity, especially agriculture focused on palm oil and rubber plantations. Primate biodiversity metrics declined most severely in Malagasy and Southeast Asian disturbed forests.

The broadscale analysis by de Almeida-Rocha et al. (2017) mirrors many studies at finer geographic scales. A study by Chapman & Lambert (2000) at Kibale National Park, Uganda, examined primate abundances at numerous locations within the park. Each of these locations had different histories of disturbance type (e.g., deforestation due to logging or agriculture) as well as varying times since disturbance. These locations included about 10% of the park as abandoned farms and 9% as disturbed forest. Based on density estimates at nearby sites, the authors estimated that these disturbed areas resulted in about a 25% reduction in the assessed primate population size. When calculating primate densities in disturbed areas, temporal lag is an important point to consider. Movement of primates from the cleared habitat to adjacent forest fragments results in artificially high densities soon after the disturbance, but these densities subsequently decline owing to insufficient resources. In a recent study using an ecological modeling approach, Wich et al. (2016) showed that orangutan abundance in Sumatra will decline to at least 67% of current levels by 2030 because of future changes in land cover patterns: specifically, predicted forest loss and fragmentation due to the increased production of agricultural land. These results emphasize the importance of careful planning for agricultural expansion, especially related to expansion into preferred habitats of endangered primates.

As has clear-cutting, increased forest fragmentation has potentially important effects on primate populations. Habitat fragmentation can alter species richness and composition, facilitate the spread of invasive species, and exacerbate human activities such as hunting and the incidence of fire (Irwin 2016, Laurance et al. 2002). Edge effects are another important consequence of fragmented habitats. Forest fragment edges may have different microclimates, increased tree mortality, and distinct dietary resources compared with that of the forest interior (Laurance et al. 2002). Lehman and colleagues (2006a) showed that lemur species responded differently to forest edges in southeastern Madagascar. *Avahi laniger* was found in higher densities closer to the forest edge, possibly owing to a combination of their folivorous nature and the increased protein content that may be found in leaves present in moderately disturbed habitats that have increased exposure to sunlight (Ganzhorn 1995). In contrast, the density of *Eulemur rufifrons* was lowest within 100 meters of the forest edge. Similarly, *Cheirogaleus major* was found at highest densities in the forest interior, and these densities declined closer to the forest edge (Lehman et al. 2006b). Even though available food was not quantified, Lehman et al. (2006b) did find that trees closer to the forest edge had relatively small diameters. If tree diameter is correlated with fruit availability, then this may be one factor to explain the reduced population density of the two most frugivorous species in edge habitats. A recent study of Neotropical primates showed a similar differential effect of edge habitats on primates with different dietary niches. Howler monkeys were found at higher densities, and spider monkeys were found at lower densities close to the forest edge (Lenz et al. 2014). Considering that most primates rely on fruit as an important component of their diet, anthropogenically induced environmental stress due to forest fragmentation may play a critical role in the survival of many primate species.

An important tool to assess the impact of habitat loss and fragmentation on primate populations is hormone analysis. Specifically, cortisol levels from primates living in disturbed and undisturbed habitats have been quantified from various biological samples, including hair, urine, and feces. Many studies have found that primate populations living in disturbed habitats have higher cortisol levels than do populations living in more pristine conditions (though see Tecot 2013 for an exception). For instance, this pattern has been demonstrated in spider monkeys (*Ateles geoffroyi*) living in the Yucatán Peninsula (Rangel-Negrín et al. 2009), gray-cheeked mangabeys (*Lophocebus albigena*) in Uganda (Jaimez et al. 2012), and male vervet monkeys across South Africa (Fourie et al. 2015).

Finally, loss of preferred habitat and habitat fragmentation may also lead to an increased frequency of hybridization among co-occurring primate species. Evidence has shown many cases of hybridization in relatively undisturbed habitats, though anthropogenically induced habitat destruction may also produce higher rates of hybridization. Detwiler (2002) found that blue monkeys (*Cercopithecus mitis*) and red-tailed monkeys (*C. ascanius*) hybridized more frequently at Gombe National Park than at four other East African study sites with these species. A possible explanation for this pattern may be the high levels of deforestation around Gombe during the past 60 years, which has, in effect, made the site an island disconnected from any other forested areas. High rates of hybridization may have varied evolutionary effects, including new lineage formation (Abbott et al. 2013, Zinner et al. 2011). Hybridization of parental species with very different population sizes could result in the effective extinction of the smaller population species through genetic swamping (Detwiler et al. 2005). In any case, the continued loss and fragmentation of primate habitats will lead to more extirpations and eventual species-level extinctions.

Climate Change

Twenty-first century climate change has been well documented, and all evidence points to an increase in global temperatures during the next several decades (IPCC 2014). Increased global temperatures associated with changing ocean currents and the jet stream will have major impacts on many habitats where primates are found. These climate and associated habitat changes are expected to occur at a rate not observed in the paleontological record. Therefore, animals with long life histories and slow reproductive rates, such as most primates, will likely suffer when their preferred habitat is no long available.

Recently published models have predicted drastically reduced geographic ranges for several primate species that are already at a high risk of extinction. Brown & Yoder (2015) generated species distribution models for 57 Malagasy primate species and found that 60% will have significantly smaller range sizes solely because of future climate change. Their findings are especially concerning given that most of these species are already at a high risk of extinction. Struebig and colleagues (2015) used a similar approach to quantify the future suitable habitat for the endangered Bornean orangutan. They predicted that the available suitable habitat will decrease by 63% by the year 2080 owing to climate change alone. This value increases to 74% when other sources of habitat change, such as deforestation, are considered. An increase in habitat fragmentation will likely have a compounding negative impact on these populations (Struebig et al. 2015). This effect is especially relevant for orangutans because females are philopatric. Therefore, their limited dispersal ability may lead to a relatively rapid reduction in genetic diversity at the population scale. Thankfully, not every study investigating the impacts of climate change on primate populations has yielded negative scenarios. Sesink Clee et al. (2015) modeled the impact of future climate change on chimpanzee populations in Nigeria and Cameroon and found varied results. Populations currently living in rainforest habitat are not predicted to show a contraction or shift in their suitable habitat. In contrast, populations living in a habitat ecotone are expected to suffer from a range contraction in each of the three future time periods modeled. If these predictions come to fruition, then important genetic diversity in West African chimpanzee populations will be lost.

Anthropogenic stressors on primate populations are often multifactorial. The combined effects of forest fragmentation, hunting, and climate change may prompt cascading effects or amplify negative feedbacks (Brook et al. 2008). For example, climate change is expected to fuel deforestation from agricultural expansion on Borneo, resulting in primate habitat loss. Warmer minimum temperatures are predicted to cause higher-elevation areas that are currently forested to become suitable for oil palm cultivation. The detrimental impact of habitat loss from the

synergistic interaction of warming climate and agricultural expansion is predicted to be worse than either threat alone or the additive combination of the two (Brodie 2016). Thus, anthropogenic threats can occur independently or in an additive way, but they can also behave synergistically. An important area of future research is to assess these simultaneous stressors and to identify the relationships between threats for primate populations of conservation concern.

Disease and Parasite Risk

Disease can be a form of environmental stress and also result from environmental stress. Evidence shows that parasites and diseases have acted as important selective forces interacting with various aspects of primate biology, including sociality, physiology, and immune function (Nunn & Altizer 2006, Nunn et al. 2015). The role of disease in affecting primate populations is now more complex owing to local-scale anthropogenic impacts, as well as human-induced effects on ecosystems and the global climate (Chapman et al. 2005). In fact, a growing body of research has demonstrated that anthropogenic effects can increase disease and parasite transmission, resulting in negative impacts on primate populations, though these patterns are often complex and not necessarily easy to predict (Young et al. 2013).

Some of the best examples of the human impact on nonhuman primate disease risk is from Africa. Gillespie and colleagues (2005) found that red-tailed monkeys in logged areas of Kibale National Park displayed increased gut parasite prevalence and species richness compared with monkeys in the unlogged forest. This finding was correlated with a declining population size of red-tailed monkeys in these same logged forests, suggesting a possible connection between health and population stability. A more recent study at the same site examined chimpanzees that were infected with rhinovirus C, a virus typically found in humans (Scully et al. 2018). This virus is a common cause of nonlethal human respiratory disease but produced severe health impacts in wild chimpanzees. Five of the approximately 56 individuals in the chimpanzee community died, and numerous other individuals showed signs of illness.

In Madagascar, Bublitz and colleagues (2015) showed that lemur species living in disturbed areas of Ranomafana National Park were associated with the presence of enteric bacterial pathogens, whereas populations inhabiting intact forests did not. These bacteria were also found in humans, livestock, and/or rodent populations. These results suggest that cross-species transmission of these bacteria to lemurs was a common occurrence. In addition, although the presence of these bacteria is a common cause of illness in humans, their impact on lemur population stability is not well established. In a related study, Zohdy and colleagues (2015) examined diarrhea-associated viruses present in seven lemur species in Ranomafana and humans living in close proximity to the lemurs. They found that 64% of the 77 lemur individuals sampled contained at least one of the 5 virus types screened (adenovirus, enterovirus, norovirus GI and GII, and rotavirus). Similarly, about 62% of the 107 humans examined also showed at least one type of virus present in their fecal samples. Their genetic analyses did not provide enough resolution to confidently determine if the viruses were being transmitted between lemurs and humans. It does further indicate, however, the similarity of viruses found in humans and related primate species, which may lend itself to cross-species transmission (Nunn 2012, Streicker et al. 2010), especially given growing human populations and increasing encroachment on primate habitats.

PRIMATE POPULATIONS MONITORED BY CAMERA TRAPS

Camera trap surveys have become a popular technique for assessing change in animal populations broadly (O'Brien 2016) and are becoming an increasingly popular tool for studying primates

(Pebsworth & LaFleur 2014). They have been used to evaluate population trends within and across protected areas and to examine the influence of anthropogenic stressors. For example, the TEAM Network surveys terrestrial mammal and bird populations on an annual basis, using a standardized protocol with large-scale arrays of permanent camera-trap points (Jansen et al. 2014). TEAM was established in 2002 to monitor long-term trends in biodiversity in tropical forest protected areas throughout the world. At each of the 17 sites, 60 camera traps have been deployed at a density of 1 camera per 1–2 km². Species with an average body mass of ≥100 g are monitored if the species spends a large proportion of its time on or near the ground or if the species is arboreal and there is at least one TEAM site where the species is detected at least 5 times during each annual survey.

The first global assessment of wildlife in tropical forest protected areas using standardized in situ data from TEAM examined the status of 511 mammal and bird populations, including 24 primate populations (Beaudrot et al. 2016). The primate populations occurred at 8 study sites located in Africa and Southeast Asia (**Supplemental Table 1**). (No primate populations were monitored at the Neotropical TEAM sites because there are no terrestrial primates in the New World.) The study used camera trap data collected between 2007 and 2014 and evaluated populations using occupancy modeling.

None of the primate populations increased significantly, and 5 of the 24 populations declined significantly. Nine populations were classified as stable. These results suggest that while none of these protected areas are currently supporting increasing primate populations, protected areas are nonetheless an important tool for conserving stable populations. The population status of 10 of the 24 populations was classified as unknown owing to a low number of detections by the camera traps. Supplemental forms of monitoring would likely improve estimates for these populations. More than half of the monitored populations are considered threatened by the International Union for Conservation of Nature (IUCN) Red List. Fortunately, most of the threatened populations had stable occupancies during the study period (**Figure 3a**). Perhaps surprisingly, none of the declining populations were hunted nor were the declining populations consistently found in isolated protected areas (**Figure 3b,c**). However, populations could have been negatively affected by

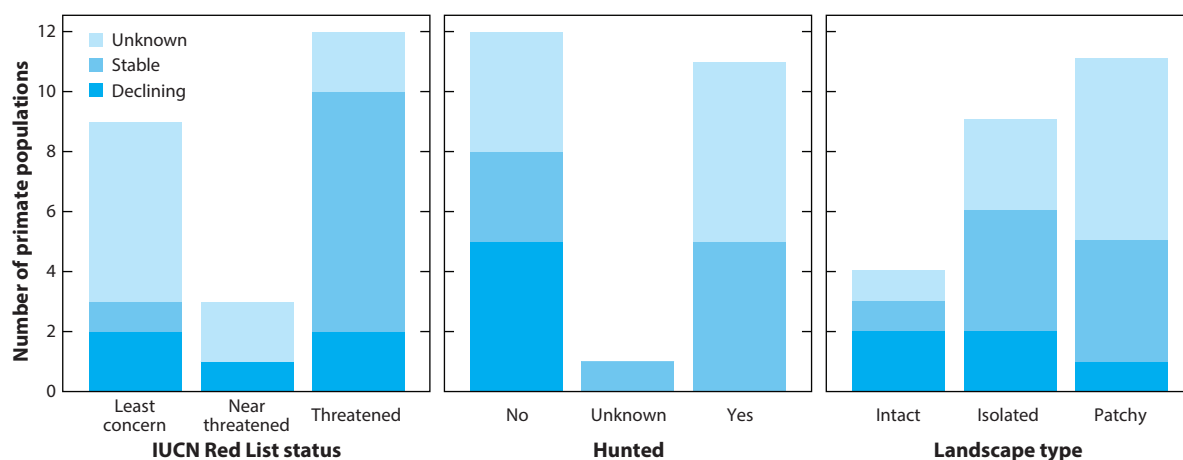


Figure 3

Population status for the 24 primate populations monitored by TEAM according to the International Union for Conservation of Nature (IUCN) Red List Status, which indicates whether a population was hunted and which is based on the connectivity of the surrounding forest. Data from Beaudrot et al. (2016). See **Supplemental Table 1** for detailed information on the primate populations.

anthropogenic disturbances prior to the onset of monitoring. Continued monitoring is necessary to determine whether the detected occupancy trends reflect short-term fluctuations or false stability. An exciting area of future research is to use camera trap data such as these to evaluate primate populations and their terrestrial predator populations simultaneously.

CONCLUSION

Primates are subject to myriad forms of environmental stress. These forms range from natural abiotic conditions, such as temperature and rainfall extremes, to the negative outcomes of interacting with members of their own species or other species. Anthropogenic impacts place further strain on free-living primate populations and can compromise population persistence. The primate species alive today have weathered previous environmental stress through behavioral plasticity, dispersal, and adaptation, but the rapid pace of global change poses unprecedented challenges for long-lived, slowly reproducing animals.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

- Abbott R, Albach D, Ansell S, Arntzen JW, Baird SJ, et al. 2013. Hybridization and speciation. *J. Evol. Biol.* 26:229–46
- Ancrenaz M, Oram F, Ambu L, Lackman I, Ahmad E, et al. 2015. Of *Pongo*, palms and perceptions: a multi-disciplinary assessment of Bornean orang-utans *Pongo pygmaeus* in an oil palm context. *Oryx* 49:465–72
- Araujo MB, Peterson AT. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93:1527–39
- Arlet ME, Isbell LA. 2009. Variation in behavioral and hormonal responses of adult male gray-cheeked mangabeys (*Lophocebus albigena*) to crowned eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behav. Ecol. Sociobiol.* 63:491–99
- Bădescu I, Wikberg EC, MacDonald LJ, Fox SA, Vayro JV, et al. 2016. Infanticide pressure accelerates infant development in a wild primate. *Anim. Behav.* 114:231–39
- Beaudrot L, Ahumada JA, O'Brien T, Alvarez-Loayza P, Boekee K, et al. 2016. Standardized assessment of biodiversity trends in tropical forest protected areas: The end is not in sight. *PLoS Biol.* 14:e1002357
- Beaudrot L, Kamilar JM, Marshall AJ, Reed KE. 2014. African primate assemblages exhibit a latitudinal gradient in dispersal limitation. *Int. J. Primatol.* 35:1088–104
- Beaudrot LH, Marshall AJ. 2011. Primate communities are structured more by dispersal limitation than by niches. *J. Anim. Ecol.* 80:332–41
- Bijlsma R, Loeschcke V. 2005. Environmental stress, adaptation and evolution: an overview. *J. Evol. Biol.* 18:744–49
- Blair ME, Sterling EJ, Dusch M, Raxworthy CJ, Pearson RG. 2013. Ecological divergence and speciation between lemur (*Eulemur*) sister species in Madagascar. *J. Evol. Biol.* 26:1790–801
- Blanco MB, Dausmann KH, Ranaivoarisoa JF, Yoder AD. 2013. Underground hibernation in a primate. *Sci. Rep.* 3:1768
- Borgerson C, McKean MA, Sutherland MR, Godfrey LR. 2016. Who hunts lemurs and why they hunt them. *Biol. Conserv.* 197:124–30
- Brockman DK, van Schaik CP, eds. 2005. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge Univ. Press
- Brodie JF. 2016. Synergistic effects of climate change and agricultural land use on mammals. *Front. Ecol. Environ.* 14:20–26

- Brodie JF, Giordano A. 2013. Lack of trophic release with large mammal predators and prey in Borneo. *Biol. Conserv.* 163:58–67
- Bronikowski AM, Altmann J. 1996. Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behav. Ecol. Sociobiol.* 39:11–25
- Brook BW, Sodhi NS, Bradshaw CJA. 2008. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* 23:453–60
- Brown JL, Yoder AD. 2015. Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecol. Evol.* 5:1131–42
- Bublitz DC, Wright PC, Rasambainarivo FT, Arrigo-Nelson SJ, Bodager JR, Gillespie TR. 2015. Pathogenic enterobacteria in lemurs associated with anthropogenic disturbance. *Am. J. Primatol.* 77:330–37
- Buckley LB, Hurlbert AH, Jetz W. 2012. Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Glob. Ecol. Biogeogr.* 21:873–85
- Cairns J Jr. 2013. Stress, environmental. In *Encyclopedia of Biodiversity*, Vol. 7, ed. SA Levin, pp. 39–44. Waltham, MA: Elsevier. 2nd ed.
- Campbell CJ. 2006. Lethal intragroup aggression by adult male spider monkeys (*Ateles geoffroyi*). *Am. J. Primatol.* 68:1197–201
- Campos FA, Fedigan LM. 2014. Spatial ecology of perceived predation risk and vigilance behavior in white-faced capuchins. *Behav. Ecol.* 25:477–86
- Campos FA, Morris WF, Alberts SC, Altmann J, Brockman DK, et al. 2017. Does climate variability influence the demography of wild primates? Evidence from long-term life-history data in seven species. *Glob. Change Biol.* 23:4907–21
- Cannon CH, Curran LM, Marshall AJ, Leighton M. 2007. Long-term reproductive behavior of woody plants across seven Bornean forest types in the Gunung Palung National Park, Indonesia: suprannual synchrony, temporal productivity, and fruiting diversity. *Ecol. Lett.* 10:956–69
- Cardini A, Jansson AU, Elton S. 2007. A geometric morphometric approach to the study of ecogeographical and clinal variation in vervet monkeys. *J. Biogeogr.* 34:1663–78
- Chapman CA, Bonnell TR, Gogarten JF, Lambert JE, Omeja PA, et al. 2013. Are primates ecosystem engineers? *Int. J. Primatol.* 34:1–14
- Chapman CA, Gillespie TR, Goldberg TL. 2005. Primates and the ecology of their infectious diseases: How will anthropogenic change affect host-parasite interactions? *Evol. Anthropol.* 14:134–44
- Chapman CA, Lambert JE. 2000. Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. *Am. J. Primatol.* 50:169–85
- Crofoot MC, Wrangham RW. 2010. Intergroup aggression in primates and humans: the case for a unified theory. In *Mind the Gap*, ed. PM Kappeler, J Silk, pp. 171–95. Berlin: Springer
- Crowley BE, Godfrey LR, Bankoff RJ, Perry GH, Culleton BJ, et al. 2017. Island-wide aridity did not trigger recent megafaunal extinctions in Madagascar. *Ecography* 40:901–12
- Crowley BE, Knott CD, Haryati S, Zulfa A, Blakely ME, Vogel ER. 2009. What urine can tell us about protein balance in wild orangutans. *Am. J. Phys. Anthropol.* 138:112–12
- Davis JT, Mengersen K, Abram NK, Ancrenaz M, Wells JA, Meijaard E. 2013. It's not just conflict that motivates killing of orangutans. *PLOS ONE* 8:e75373
- de Almeida-Rocha JM, Peres CA, Oliveira LC. 2017. Primate responses to anthropogenic habitat disturbance: a pantropical meta-analysis. *Biol. Conserv.* 215:30–38
- Detwiler KM. 2002. Hybridization between red-tailed monkeys (*Cercopithecus ascanius*) and blue monkeys (*C. mitis*) in East African forests. In *The Guenons: Diversity and Adaptation in African Monkeys*, ed. M Glenn, M Cords, pp. 79–97. New York: Kluwer Acad/Plenum Publ.
- Detwiler KM, Burrell AS, Jolly CJ. 2005. Conservation implications of hybridization in African cercopithecine monkeys. *Int. J. Primatol.* 26:661–84
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghilambor CK, et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS* 105:6668–72
- Dewar RE, Richard AF. 2007. Evolution in the hypervariable environment of Madagascar. *PNAS* 104:13723–27
- Dunham AE, Erhart EM, Wright PC. 2011. Global climate cycles and cyclones: consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. *Glob. Change Biol.* 17:219–27

- Ebensperger LA. 1998. Strategies and counterstrategies to infanticide in mammals. *Biol. Rev.* 73:321–46
- Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, et al. 2017. Impending extinction crisis of the world's primates: why primates matter. *Sci. Adv.* 3:e1600946
- Fa JE, Garcia Yuste JE, Castelo R. 2000. Bushmeat markets on Bioko Island as a measure of hunting pressure. *Conserv. Biol.* 14:1602–13
- Fleagle JG. 2013. *Primate Adaptation and Evolution*. San Diego: Academic
- Fourie NH, Turner TR, Brown JL, Pampush JD, Lorenz JG, Bernstein RM. 2015. Variation in vervet (*Chlorocebus aethiops*) hair cortisol concentrations reflects ecological disturbance by humans. *Primates* 56:365–73
- Ganzhorn JU. 1995. Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology* 76:2084–96
- Ganzhorn JU, Klaus S, Ortmann S, Schmid J. 2003. Adaptations to seasonality: some primate and nonprimate examples. In *Primate Life Histories and Socioecology*, ed. PM Kappeler, ME Pereira, pp. 132–44. Chicago: Univ. Chicago Press
- Gillespie TR, Chapman CA, Greiner EC. 2005. Effects of logging on gastrointestinal parasite infections and infection risk in African primates. *J. Appl. Ecol.* 42:699–707
- Godfrey LR, Irwin MT. 2007. The evolution of extinction risk: past and present anthropogenic impacts on the primate communities of Madagascar. *Folia Primatol.* 78:405–19
- Gordon AD, Johnson SE, Louis EE. 2013. Females are the ecological sex: sex-specific body mass ecogeography in wild sifaka populations (*Propithecus spp.*). *Am. J. Phys. Anthropol.* 151:77–87
- Gros-Louis J, Perry S, Manson JH. 2003. Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). *Primates* 44:341–46
- Harrison T, Krigbaum J, Manser J. 2006. Primate biogeography and ecology on the Sunda Shelf islands: a paleontological and zooarchaeological perspective. See Lehman & Fleagle 2006, pp. 331–74
- Hernández-Pacheco R, Rawlins RG, Kessler MJ, Williams LE, Ruiz-Maldonado TM, et al. 2013. Demographic variability and density-dependent dynamics of a free-ranging rhesus macaque population. *Am. J. Primatol.* 75:1152–64
- Hill CM. 2000. Conflict of interest between people and baboons: crop raiding in Uganda. *Int. J. Primatol.* 21:299–315
- IPCC (Intergov. Panel Clim. Change). 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva: IPCC. http://www.ipcc.ch/pdf/assessment-report/ar5/syr/SYR_AR5_FINAL_full_wcover.pdf
- Irwin M. 2016. Habitat change: loss, fragmentation, and degradation. See Wich & Marshall 2016, pp. 111–28
- Isbell LA. 1990. Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park, Kenya. *Am. J. Primatol.* 21:41–52
- Jablonski NG, Chaplin G. 2010. Human skin pigmentation as an adaptation to UV radiation. *PNAS* 107:8962–68
- Jaimez NA, Bribiescas RG, Aronsen GP, Anestis SA, Watts DP. 2012. Urinary cortisol levels of gray-cheeked mangabeys are higher in disturbed compared to undisturbed forest areas in Kibale National Park, Uganda. *Anim. Conserv.* 15:242–47
- Jansen PA, Ahumada J, Fegraus E, O'Brien T. 2014. TEAM: a standardised camera trap survey to monitor terrestrial vertebrate communities in tropical forests. In *Camera Trapping: Wildlife Management and Research*, ed. PD Meek, PJS Fleming, pp. 263–70. Melbourne, Aust.: CSIRO
- Janzen DH. 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101:233–49
- Kamilar JM. 2009. Environmental and geographic correlates of the taxonomic structure of primate communities. *Am. J. Phys. Anthropol.* 139:382–93
- Kamilar JM, Baden AL. 2014. What drives flexibility in primate social organization? *Behav. Ecol. Sociobiol.* 68:1677–92
- Kamilar JM, Beaudrot L. 2013. Understanding primate communities: recent developments and future directions. *Evol. Anthropol.* 22:174–85
- Kamilar JM, Blanco MB, Muldoon KM. 2016. Ecological niche modeling of mouse lemurs (*Microcebus spp.*) and its implications for their species diversity and biogeography. In *Dwarf and Mouse Lemurs of Madagascar: Biology, Behavior and Conservation Biogeography of the Cheirogaleidae*, ed. SM Lehman, U Radespiel, E Zimmermann, pp. 449–61. Cambridge, UK: Cambridge Univ. Press

- Kamilar JM, Bradley BJ. 2011. Interspecific variation in primate coat color supports Gloger's rule. *J. Biogeogr.* 38:2270–77
- Kamilar JM, Marshack JL. 2012. Does geography or ecology best explain 'cultural' variation among chimpanzee communities? *J. Hum. Evol.* 62:256–60
- Kamilar JM, Martin SK, Tosi AJ. 2009. Combining biogeographic and phylogenetic data to examine primate speciation: an example using Cercopithecine monkeys. *Biotropica* 41:514–19
- Kamilar JM, Muldoon KM, Lehman SM, Herrera JP. 2012. Testing Bergmann's rule and the resource seasonality hypothesis in Malagasy primates using GIS-based climate data. *Am. J. Phys. Anthropol.* 147:401–8
- Kamilar JM, Tecot SR. 2016. Anthropogenic and climatic effects on the distribution of *Eulemur* species: an ecological niche modeling approach. *Int. J. Primatol.* 37:47–68
- Kay RF, Madden RH, van Schaik C, Higdson D. 1997. Primate species richness is determined by plant productivity: implications for conservation. *PNAS* 94:13023–27
- Khaliq I, Hof C, Prinzing R, Bohning-Gaese K, Pfenninger M. 2014. Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proc. R. Soc. B* 281:20141097
- Knott CD. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *Int. J. Primatol.* 19:1061–79
- Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, et al. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* 16:605–18
- Lehman SM, Fleagle JG, eds. 2006. *Primate Biogeography*. New York: Springer
- Lehman SM, Rajaonson A, Day S. 2006a. Edge effects and their influence on lemur density and distribution in Southeast Madagascar. *Am. J. Phys. Anthropol.* 129:232–41
- Lehman SM, Rajaonson A, Day S. 2006b. Edge effects on the density of *Cheirogaleus major*. *Int. J. Primatol.* 27:1569–88
- Lenz BB, Jack KM, Spironello WR. 2014. Edge effects in the primate community of the biological dynamics of Forest Fragments Project, Amazonas, Brazil. *Am. J. Phys. Anthropol.* 155:436–46
- Lewis RJ, Kappeler PM. 2005. Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. *Am. J. Primatol.* 67:347–64
- Linder JM, Oates JF. 2011. Differential impact of bushmeat hunting on monkey species and implications for primate conservation in Korup National Park, Cameroon. *Biol. Conserv.* 144:738–45
- Lutz W, Butz WP, Samir KC, eds. 2017. *World Population and Human Capital in the Twenty-First Century: An Overview*. Oxford, UK: Oxford Univ. Press
- MacArthur RH, Diamond JM, Karr JR. 1972. Density compensation in island faunas. *Ecology* 53:330–42
- Marshall AJ, Leighton M. 2006. How does food availability limit the population density of white-bearded gibbons? In *Feeding Ecology of the Apes*, ed. G Hohmann, MM Robbins, C Boesch, pp. 313–35. Cambridge, UK: Cambridge Univ. Press
- Marshall AJ, Wich SA. 2016. Some future directions for primate conservation research. See Wich & Marshall 2016, pp. 287–96
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–58
- Nunn CL. 2012. Primate disease ecology in comparative and theoretical perspective. *Am. J. Primatol.* 74:490–509
- Nunn CL, Altizer SM. 2006. *Infectious Diseases in Primates: Behavior, Ecology and Evolution*. Oxford, UK: Oxford Univ. Press
- Nunn CL, Craft ME, Gillespie TR, Schaller M, Kappeler PM. 2015. The sociality–health–fitness nexus: synthesis, conclusions and future directions. *Phil. Trans. R. Soc. B* 370:20140115
- O'Brien T. 2016. Camera traps for conservation: monitoring protected area investments. In *Protected Areas: Are They Safeguarding Biodiversity?*, ed. LN Joppa, IEM Baillie, JG Robinson, pp. 228–41. Hoboken, NJ: Wiley-Blackwell
- Palombit RA. 1993. Lethal territorial aggression in a white-handed gibbon. *Am. J. Primatol.* 31:311–18
- Pebsworth PA, LaFleur M. 2014. Advancing primate research and conservation through the use of camera traps: introduction to the special issue. *Int. J. Primatol.* 35:825–40
- Peres CA. 1990. Effects of hunting on western Amazonian primate communities. *Biol. Conserv.* 54:47–59

- Peres CA, Dolman PM. 2000. Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* 122:175–89
- Peres CA, Palacios E. 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* 39:304–15
- Peterson D. 2003. *Eating Apes*. London: Univ. Calif. Press
- Rangel-Negrin A, Alfaro JL, Valdez RA, Romano MC, Serio-Silva JC. 2009. Stress in Yucatan spider monkeys: effects of environmental conditions on fecal cortisol levels in wild and captive populations. *Anim. Conserv.* 12:496–502
- Raxworthy CJ, Ingram CM, Rabibisoa N, Pearson RG. 2007. Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. *Syst. Biol.* 56:907–23
- Reed KE, Fleagle JG. 1995. Geographic and climatic control of primate diversity. *PNAS* 92:7874–76
- Roberts EK, Lu A, Bergman TJ, Beehner JC. 2012. A Bruce effect in wild geladas. *Science* 335:1222–25
- Rowan J, Kamilar JM, Beaudrot L, Reed KE. 2016. Strong influence of palaeoclimate on the structure of modern African mammal communities. *Proc. R. Soc. B* 283:20161207
- Scully EJ, Basnet S, Wrangham RW, Muller MN, Otali E, et al. 2018. Lethal respiratory disease associated with human rhinovirus C in wild chimpanzees, Uganda, 2013. *Emerg. Infect. Dis.* 24:267–74
- Sesink Clee PR, Abwe EE, Ambahe RD, Anthony NM, Fotso R, et al. 2015. Chimpanzee population structure in Cameroon and Nigeria is associated with habitat variation that may be lost under climate change. *BMC Evol. Biol.* 15:2
- Shultz S, Finlayson LV. 2010. Large body and small brain and group sizes are associated with predator preferences for mammalian prey. *Behav. Ecol.* 21:1073–79
- Soares-Filho BS, Nepstad DC, Curran LM, Cerqueira GC, et al. 2006. Modelling conservation in the Amazon basin. *Nature* 440:520–23
- Streicker DG, Turmelle AS, Vonhof MJ, Kuzmin IV, McCracken GF, Rupprecht CE. 2010. Host phylogeny constrains cross-species emergence and establishment of rabies virus in bats. *Science* 329:676–79
- Strier KB. 2017. What does variation in primate behavior mean? *Am. J. Phys. Anthropol.* 162:4–14
- Strier KB, Ziegler TE, Wittwer DJ. 1999. Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis (*Brachyteles arachnoides*). *Horm. Behav.* 35:125–34
- Struebig MJ, Fischer M, Gaveau DLA, Meijaard E, Wich SA, et al. 2015. Anticipated climate and land-cover changes reveal refuge areas for Borneo's orang-utans. *Glob. Change Biol.* 21:2891–904
- Strum SC. 2010. The development of primate raiding: implications for management and conservation. *Int. J. Primatol.* 31:133–56
- Tecot SR. 2013. Variable energetic strategies in disturbed and undisturbed rain forest habitats: *Eulemur rubriventer* fecal cortisol levels in southeastern Madagascar. In *Leaping Ahead: Advances in Prosimian Biology*, ed. J Masters, M Gamba, F Génin, R Tuttle, pp. 185–95. New York: Springer
- Terborgh J, Lopez L, Nuñez P, Rao M, Shahabuddin G, et al. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923–26
- Thompson ME, Knott CD. 2008. Urinary C-peptide of insulin as a non-invasive marker of energy balance in wild orangutans. *Horm. Behav.* 53:526–35
- Thorn JS, Nijman V, Smith D, Nekaris KAI. 2009. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (*Primates: Nycticebus*). *Divers. Distrib.* 15:289–98
- Valero A, Schaffner CM, Vick LG, Aureli F, Ramos-Fernandez G. 2006. Intragroup lethal aggression in wild spider monkeys. *Am. J. Primatol.* 68:732–37
- Watts DP, Amsler SJ. 2013. Chimpanzee-red colobus encounter rates show a red colobus population decline associated with predation by chimpanzees at Ngogo. *Am. J. Primatol.* 75:927–37
- West-Eberhard MJ. 2003. *Developmental Plasticity and Evolution*. New York: Oxford Univ. Press
- Wich SA, Marshall AJ, eds. 2016. *An Introduction to Primate Conservation*. Oxford, UK: Oxford Univ. Press
- Wich SA, Singleton I, Nowak MG, Atmoko SSU, Nisam G, et al. 2016. Land-cover changes predict steep declines for the Sumatran orangutan (*Pongo abelii*). *Sci. Adv.* 2:e1500789
- Willems EP, Hill RA. 2009. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology* 90:546–55

- Wilson ML, Boesch C, Fruth B, Furuichi T, Gilby IC, et al. 2014. Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature* 513:414–17
- Young H, Griffin RH, Wood CL, Nunn CL. 2013. Does habitat disturbance increase infectious disease risk for primates? *Ecol. Lett.* 16:656–63
- Zinner D, Arnold ML, Roos C. 2011. The strange blood: natural hybridization in primates. *Evol. Anthropol.* 20:96–103
- Zohdy S, Grossman MK, Fried IR, Rasambainarivo FT, Wright PC, Gillespie TR. 2015. Diversity and prevalence of diarrhea-associated viruses in the lemur community and associated human population of Ranomafana National Park, Madagascar. *Int. J. Primatol.* 36:143–53