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Primate Foraging Strategies Modulate Responses to Anthropogenic Change and Thus Primate Conservation

Colin A. Chapman, Kim Valenta, Fabiola Espinosa-Gomez, Amelie Corriveau and Sarah Bortolamiol

On October 17, 2022, the World Wildlife Fund announced that the world had lost 69% of its biodiversity over the past 50 years, and it is estimated that we are losing approximately 11,000-58,000 species annually (Dirzo et al. 2014; WWF 2022). Primate species may also have been lost (McGraw 2005; Oates, Abedi-Lartey, et al. 2000), and many are on the brink of extinction (Estrada, Garber, et al. 2017; Mittermeier, Reuter, et al. 2022). In fact, it is estimated that close to 50% of the world's primates are at risk of extinction (Estrada 2013; Estrada, Garber, et al. 2017; Mittermeier, Reuter, et al. 2022), with, mately, these changes are driven by increased human population size and consumption rates. The UN Population Division estimates that the world's population is expected to rise from 7 billion in 2011 to 9 billion in 2050. Making the situation more dire for primates is the fact that, in the three primate range regions, the human population growth rate between 1980 and 2005 was 2.7% per year, well above that of European countries (0.2% per year; Estrada 2013). Thus, the human population will double in regions with primates in less than 30 years. In a global the IUCN Red List database considering 42% critically endangered. Primates face threats on multiple fronts, but likely the most significant is habitat loss (Chapman and Peres 2021). Between 2000 and 2012, it is estimated that 2.3 million km² of forest were lost globally (approximately the size of the Democratic Republic of the Congo), and, in the tropics, forest loss increased by 2,101 km² per year (M. Hansen et al. 2013). The loss is greatest in South America and Africa (fig. 29.1). Primate species loss corresponds with an increase in agriculture and cropland in tropical countries, which expanded by 48,000 km² per year between 1999 and 2008, largely at the expense of forest (Phalan et al. 2013). One estimate suggests that approximately 1 billion ha of additional land (an area larger than Canada), primarily in developing countries, will need to be converted to agriculture by 2050 to meet the demands of the growing human population (Laurance, Sayer, and Cassman 2014). Using a 1 km² resolution of the changes that occurred between 1993 and 2009, the human population size increased by 23%, the world economy grew by 153%, and the human footprint increased by 9% (Venter et al. 2016). This has resulted in 75% of the earth's land surface being impacted, with most of the unexploited areas being in the far north and in desert ecosystems. All these measures suggest that the situation for primates is grave and conservation actions must be initiated-but which ones? In the past, conservation biologists have typically responded to change and attempted to take corrective action after negative situations have occurred (Caughley 1994; Chapman and Peres 2001), but it would be much more effective if researchers were able to predict negative changes prior to their occurrence and proactively prevent animal population declines. It can be easier to prevent declines than to rebuild populations. Furthermore, population decline can lead to further detrimental effects such as increased risk of disease in small populations or loss of genetic potential (i.e., inbreeding causes loss of genetic diversity) and must be considered in conservation and management plans. To predict declines and not simply respond to changes, conservation biologists must find general patterns across taxa and locations. However, predicting change has proved difficult.

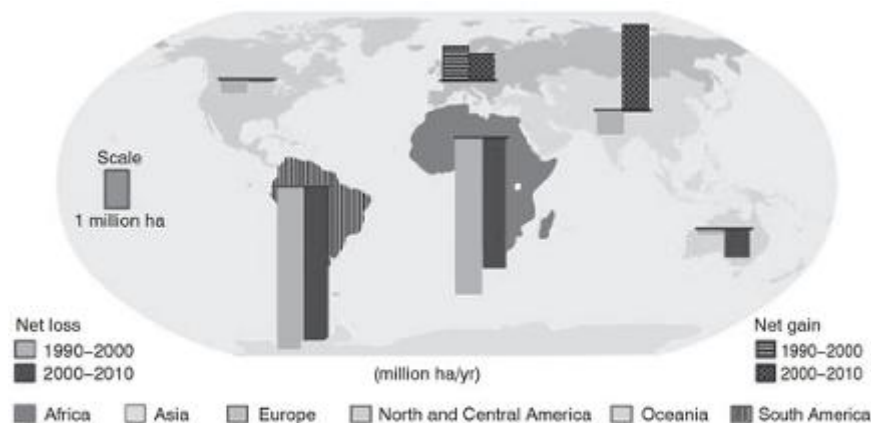


Figure 29.1. Annual change in forest area by region, 1990-2010 (from FAO 2010; reprinted with permission). These net gain values include plantation forest and forests lost to fire, but positive gains cannot represent regeneration of old-growth forest, as this would take hundreds of years.

We are ethically obligated to take conservation action, and conservation practitioners need to predict negative changes prior to their occurrence. It is common sense that understanding foraging strategies and nutritional needs is a tool that would allow conservation biologists to predict which species are most vulnerable to negative human activities and that this understanding would facilitate effective action. It would be desirable if broad generalizations could be made; for example, frugivores are more vulnerable than folivores (Oates 1996). With such generalizations in hand, setting conservation priorities and constructing management plans could be easily done. However, such generalizations have proved elusive, and, in our opinion, they are impractical to make at this time. This is because any particular population is faced with a myriad of anthropogenic and natural changes, and thus identifying the effect of one factor is impractical. For example, consider the following comparison between two populations. One folivore population (Population 1) is in an area where the local community does not hunt, is only slightly adversely impacted by climate change (Rothman, Chapman, Struhsaker, et al. 2015), and benefits from the secondary growth associated with logging (Coley 1983; Ganzhorn 1992; Oates 1996). This population would be expected to increase in abundance after the disturbance caused by timber extraction. A second population (Population 2) of the same species that is hunted during the logging operation (Brodie, Giordano, et al. 2015), is in an area with the same degree of climate change, and similarly benefits from logging would be expected to decrease in abundance after logging because of hunting. As it is so difficult to quantify historical hunting patterns, the effect of the hunting may be largely unknown and unquantified. Therefore, a comparison of the two populations examining the effects of logging would produce little meaningful understanding. Similarly, comparisons of Population 1 where the timber extraction removed mostly nonfood trees with Population 2 where mostly food trees were removed would not be meaningful without those details of what was removed. If Populations 1 and 2 experienced similar hunting, climate change, and logging, but Population 1 was monitored 1 year after the logging and Population 2 was monitored 10 years after logging, again comparisons would be meaningless. We suggest that the details needed to make meaningful comparisons are often unknown, making large literature reviews of questionable use. A comparison of two studies exemplifies the divergent outcomes that can occur. A. D. Johns (1992) studied the effects of logging on frugivorous primate populations in dipterocarp forests in Peninsular Malaysia, while E. Bennett and Dahaban (1995) addressed the same question in dipterocarp forests in Sabah. The intensity of logging was similar in the two regions. In Sabah, the logging produced an immediate 35%-70% decline in the gibbon (*Hylobates muelleri*) and langur populations (*Presbytis* spp., only partially frugivorous; E. Bennett and Dahaban 1995). In contrast, survival of the same genera in Peninsular Malaysia was much greater (10% decline to an increase of 74%; A.D. Johns 1983). We do not attempt

to state generalities, such as asserting that folivores have a lower risk of vulnerability than frugivores (Oates 1996). Rather, our objective is to outline trends in global threats to primates and predict how primates with different dietary needs and foraging strategies will respond to each threat. We consider three global threats : habitat destruction through logging and fragmentation, climate change, and bushmeat hunting. We conclude by pointing out gaps in our knowledge and by considering future research directions that would be helpful if foraging studies are to contribute to the conservation of primates.

HABITAT DESTRUCTION THROUGH LOGGING AND FOREST FRAGMENTATION

Trends

Deforestation rates are staggering (M. Hansen et al. 2013). Much of this loss can be either directly or indirectly attributed to logging and activities that timber extraction facilitated. Globally, logging shows no signs of slowing down, and thus more land that sustains primates is being destroyed each year (Estrada 2013; Estrada, Garber, et al. 2017; D. Kim et al. 2015). Between 1960 and 2010, industrial round-wood production increased from 28 million m³ to 155 million m³ in Central and South America, from 23 million m³ to 71 million m³ in sub-Saharan Africa, and from 15 million m³ to 30 million m³ in Southeast Asia (Estrada 2013). Approximately one cubic meter results from harvesting two tropical trees that are about 10-15 m tall and 60 cm in diameter; thus, the 30 million m³ harvested in South Asia comes from approximately 60 million trees of this size. Additional trees are killed during the extraction process; the number of total tree deaths is alarming. When logging is conducted, a recovery time is set within which the forest is expected to regain its basal area, at which time the area is scheduled to be logged again. In most cases, these logged areas are not left to recover; rather, they are converted to agricultural land. However, if they are not further disturbed, recent studies demonstrate that tree regeneration following logging is slower than expected or even arrested entirely. In Kibale National Park, Uganda, many abandoned logging gaps showed little forest recovery 40 years after selective logging was concluded (Chapman and Chapman 2004; Lawes and Chapman 2006; J. Paul et al. 2004). In Budongo Forest Reserve, Uganda, Plumptre (1996) found that 50 years of regeneration was insufficient for forest structure to recover to unlogged levels. Similarly, data from Bolivia indicate that the growth rate of timber trees was insufficient for similar wood volumes to be cut in the next planned harvest, and estimated recoverable volumes in the second harvest ranged from 4% to 28% of the potentially harvestable volume in the first cycle (Dauber et al. 2005). Slow rates of recovery reduce the value of logged forests. Furthermore, when logging operations revisit a concession that they previously logged after the rotation period has ended, they harvest a broader range of species than they had previously, including species, for example, from the important *Ficus* genus. Large-scale commercial harvesting of *Ficus* has been documented in Bolivia and to a lesser extent in Peru and Brazil. In Bolivia, extraction volumes of fig trees increased steadily since records began in 1998 but plateaued in the economic downturn of 2008-2009 (Felton, Felton, Rumiz, et al. 2013). Small-scale removal of *Ficus* has also been documented in Uganda (Felton, Felton, Rumiz, et al. 2013), where *Ficus* are considered important food sources, including as fallback foods, for many frugivorous primates (J. Lambert 2007, 2009) and are also important foods for folivores (Fashing 2001; Pavelka and Behie 2005).

Predicted Responses of Primates with Different Foraging Strategies to Habitat Destruction

Logging results in the removal of the targeted timber trees and substantial damage to other trees because of the damage done when getting equipment to the felled tree, when the targeted tree falls, and when the timber tree is taken out. The consequences of logging for primates are many, they are often interacting, and the processes that are altered change on different timescales. Initially, logging

(1) causes a reduction of food resources for all primates; (2) increases travel costs as animals attempt to find new food sources (Rode, Chapman, McDowell, et al. 2006) and navigate around canopy gaps (Gebo and Chapman 1995)-some species may reduce group size, permitting reduced travel costs, but others may not be able to because of the increased predation risk associated with smaller groups (Norscia, Carrai, and Borgogini-Tarli 2006); (3) causes increased intergroup conflict for territorial species, possibly involving lethal intergroup contact (J. Mitani and Watts 2005a); and (4) causes changes in stress and health status (T. Gillespie et al. 2005). Within a few years of logging, the forest begins to show significant signs of regeneration, and primates with different dietary needs are differentially able to take advantage of the regrowth. Folivorous primates often benefit first following disturbance by feeding on this regeneration, as the leaves of secondary-growth tree species are often high in protein, low in fiber, and only poorly chemically protected (Coley 1983; but see Gogarten, Guzman, et al. 2012). At this time in the forest regeneration process, folivore abundance may be higher than in neighboring old-growth areas (A. Davies 1994; Fashing 2011; Oates 1996; Plumptre and Reynolds 1994). The patterns of change in folivore populations following logging provide a useful illustration of how the evaluation of responses to logging depends on the temporal scale evaluated. Immediately following logging, folivore populations likely decline as a result of the disturbance that the logging causes, possible bushmeat harvest associated with the presence of the loggers, and loss of feeding trees. After a few years of secondary growth, trees that are trying to grow rapidly and thus do not invest in toxic leaf defenses (Coley 1983) are available at significant densities, and the folivore populations will likely rise (Oates 1977; Struhsaker 1997). Over time, these secondary-growth trees will senesce and die out (Chapman, Jacob, et al. 2010), which may in turn lead to a decline in folivore populations. The extent and speed at which secondary-growth trees arrive and grow depend on the evolutionary history of the trees in the region (P. Richards 1996) . For example, hurricane forests that are disturbed every decade or so will be rapidly colonized by many secondary-growth species that grow rapidly, while other forests will respond more slowly (Boucher 1990; Chapman, Chapman , Kaufman, et al. 1999; Ganzhorn 1995b; P. Richards 1996). The appropriate temporal scale to use will depend on the question being asked. It should also be kept in mind that any pattern of animal abundance that these responses to logging generate can be significantly modified or even totally reversed by the effects of bushmeat hunting or climate change. In addition to these direct effects (i.e., the removal of feeding species), industrial logging leads to the construction of roads that promote total deforestation through subsequent agricultural development and cattle ranching (R. Butler and Laurance 2008; Laurance, Clements, et al. 2014). The nutritional requirements of specific primates should be used by managers to guide pre-and postlogging practices. For example, important feeding trees should be left standing in selective logging operations, and loggers should use directional felling to reduce impacts on important food resources (Putz et al . 2000). Adopting such management practices may result in lowering the population declines of primates that are negatively impacted by logging or speeding population recovery. For folivores, there is a robust model predicting their abundance or biomass that can be applied to their management. Milton (1979) suggested that the protein and fiber content of leaves was an important criterion for leaf choice for small-bodied arboreal mammals such as colobines. Fiber is fermented by symbiotic microbes in the gastrointestinal tract, and some fiber components are only partially digestible; thus, animals do not select a high-fiber diet (McNab 2002). In contrast, nitrogen is a limiting nutrient in most environments and is predominantly found in protein; thus, herbivores should choose foods high in protein and low in fiber (T. C. White 1993). This influential idea has been successfully applied, and the index of protein to fiber of dominant trees in a forest predicts the abundance and biomass of folivorous monkeys at both local (Chapman and Chapman 2002; Ganzhorn 2002) and regional scales (Chapman, Chapman, Naughton-Treves, et al. 2004; A. Davies 1994; Fashing et al. 2007; Oates, Whitesides, et al. 1990; Waterman, Ross, et al. 1988). Combining all

existing data, this ratio accounts for 87% of the variance in colobine biomass (Chapman, Chapman, Naughton-Treves, et al. 2004). Similarly, an assessment across nine locations in Southeast Asia revealed a correlation between the abundance of leguminous trees and *Presbytis* biomass (A. Davies 1994), presumably because of their high leaf protein content. However, the protein-to-fiber model is controversial due to four issues (reviewed by I. Wallis et al. 2012). First, the studies used to test this protein/fiber model are all correlative (Chapman, Chapman, Jacob, et al. 2010; Chapman, Struhsaker, et al. 2010; I. Wallis et al. 2012). Second, the protein levels of leaves that colobines feed on in the wild are higher than their believed requirements (Oftedal 1991; Rothman, Raubenheimer, and Chapman 2011). Third, available nitrogen should be used to evaluate these ideas, and this is typically not done (Rothman, Chapman, and Pell 2008; Rothman, Chapman, and Van Soest 2012; I. Wallis et al. 2012). Finally, new empirical data call into question the generality of this model (Chapman, Chapman, Jacob, et al. 2010; Chapman, Struhsaker, et al. 2010; Gogarten, Guzman, et al. 2012). With respect to predicting frugivore abundance, there are fewer comparative papers and no general model; however, frugivore abundance is related to the density of fruit resources. For example, a correlation was found across six sites between chimpanzee (*Pan troglodytes*) nest density and large, fleshy-fruit tree density (Balcomb et al. 2000; see also Chapman, Chapman, and Gillespie, et al. 2002 for a similar result with a frugivorous/insectivorous primate), and chimpanzee density is higher where fig basal area is higher (Bortolamiol et al. 2014; but see Lacroux et al. 2022 for insights into other factors affecting chimpanzee habitat use). In general, it is well known that figs are important for many species of primates, other mammals, and birds (Bleher et al. 2003; Diaz-Martin et al. 2014; Janzen 1979a), while their commercial harvesting is on the rise (Felton, Felton, Rumiz, et al. 2013). Figs contain many essential nutrients and minerals (O'Brien, Kinnaird, and Dierenfeld 1998) and can provide a nutritionally balanced staple food in some areas (Felton, Felton, Wood, Foley, et al. 2009). While there is no evidence that figs act as keystone species (Chapman, Chapman, Struhsaker, et al. 2005; Gautier-Hion and Michaloud 1989), ripe fruits are eaten by many frugivorous primates (O'Brien, Kinnaird, and Dierenfeld 1998), and folivores often eat unripe fruits or fig leaves (Dasilva 1994; Milton, Morrison, et al. 1982). Not only is there loss in the total surface area of oldgrowth forest, but it is also being fragmented at an accelerating rate (L. Marsh and Chapman 2013; UNEP 2001). Forest fragmentation often leaves primates with a very low diversity of food species (exacerbated by climate change; see below). This is illustrated by two examples from Western Uganda, where deforestation outside of national parks has been extensive. A group of over 20 red colobus (*Piliocolobus tephrosceles*) living along a riverine strip of forest with extremely low plant diversity spent 91.9% of their foraging time eating from one species of tree (Chapman, Chapman and Gillespie 2002). This group survived under these conditions for at least four years, until the riverine forest was largely cleared for timber. Similarly, in a very degraded fragment, a group of four to six red colobus survived in an area containing only seven trees with a diameter at breast height of 10 cm or greater, and they survived for over 15 years (Chapman, Ghai, et al. 2013). In some cases, remaining forest fragments may be too small to meet the nutritional requirements of primates, forcing them to forage in the matrix. In Mexico, black howlers (*Alouatta pigra*) live in fragments as small as 0.4 ha, and the paucity of essential foods and specific nutrients probably forces them to travel to scattered trees in pastures. This matrix foraging puts them at risk of predation, including from domesticated animals such as dogs (Pozo-Montuy et al. 2013). The construction of corridors of trees is one means of removing this danger, and corridors have been a major aspect of a number of conservation projects (T. Jones et al. 2012; Noss 1995). In restoration projects, these corridors could be planted with important food trees, and the choice of these trees can be directly guided by the knowledge gained by research focused on the feeding ecology conducted on primate species of special concern. A complication in many areas of the world is that primates in fragments are hunted, further decreasing the conservation value of forest fragments (Benchimol and Peres 2013a, 2013b).

CLIMATE CHANGE

Trends

The earth's climate has warmed significantly as the result of human actions. The Intergovernmental Panel on Climate Change estimates that the earth's climate has warmed by 1.2°C since industrialization, and by the end of the 21st century the earth's mean surface temperature is set to increase by at least 1.5°C (IPCC 2021). Rising temperature alters global patterns of circulation, which affects rainfall patterns, but changes do not occur uniformly around the earth (Graham et al. 2016). Given where primates occur, they will experience 10% more warming than the global mean (Graham et al. 2016). Precipitation changes will also likely be quite varied across primate ranges (from >7.5% increases per °C of global warming to >7.5% decreases; Graham et al. 2016). To date, there have been numerous documented shifts in plant and animal distributions, population abundance, life history, and survival of species in response to climate change (Hannah et al. 2002; Newman et al. 2011; Pounds et al. 1999). Short-term extremes such as droughts and floods will affect plants, animals, and human populations, and such events will come more frequently and be more intense with climate change. In fact, droughts have already increased in frequency and intensity since the 1970s (N. Watts et al. 2021). While changes that will have an obvious effect on primate populations are of great concern (e.g., loss of habitat because of drying and heat stress), it is also important to proactively seek to understand the subtle, unexpected, or cascading effects of climate change (see also Rothman et al., this volume). One such unanticipated effect of climate change may be alterations in the nutritional quality of plant parts, in particular the leafy food resources of folivorous primates (Coley et al. 2002). Current knowledge of how plants respond to changes in climate (CO₂ levels, temperature, and rainfall) is based on greenhouse experiments, and results vary depending on plant species and soil nutrients; however, in general, experiments demonstrate that increased temperature and elevated CO₂ levels result in a reduction in leaf protein and an increase in fiber (Buse et al. 1998; Curtis and Wang 1998; Dury et al. 1998; Kanowski 2001; E. Robinson et al. 2012; Zvereva and Kozlov 2006). In addition, analysis of tropical trees along a rainfall gradient revealed that nitrogen content (mostly protein) decreased and nitrogen-to-fiber ratios decreased with increasing precipitation (Santiago and Mulkey 2005). Similar effects on leaf chemistry have been found for increasing temperature (Craine, Elmore, Olson, et al. 2010; Weih and Karlsson 2001). A significant proportion of the nitrogen in a leaf is protein, so the protein-to-fiber model described earlier predicts that this nitrogen decline will have negative consequences for the nutrition of folivorous primates. For primates that rely on insects, studies have found that insect populations respond to climate change with changes in range, abundance, and phenology (reviewed in Andrew et al. 2013). In fact, one study of insects in southern Africa forecasts reduced insect diversity as a consequence of abiotic changes resulting from climate change (Pio et al. 2014).

Predicted Responses of Primates with Different Foraging Strategies to Climate Change

Understanding the consequences of climate change for primates may be the most important question that primate conservation biologists must address in the next decade; however, our ability to predict primate responses to climate change is very poor (P. Wright 2007). It is relatively easy to imagine that in areas becoming hotter and drier, primates will become physiologically stressed (McFarland, Barrett, Boner, et al. 2014), food trees will die, and primates will die along with them or be forced to move if fragmentation is not severe enough to make that impossible. This is supported by data from Amboseli National Park, Kenya, where the average daily maximum temperature increased by 0.275°C per year (an order of magnitude greater than that predicted by climate change models; J. Altmann et al. 2002) and there was a dramatic loss of tree cover (J. Altmann et al. 2002), which may have driven the concomitant decline in local vervet populations and movement of baboon

populations (Struhsaker 1973). The hotter temperatures associated with climate change may trigger a short-term regulatory response in primates that may change what they need to eat (Raubenheimer, Simpson, and Tait 2012). For example, primates living under hotter temperatures may select foods with a higher water or salt content. Many primates have been shown to have low salt intake and to eat unusual foods, such as decaying wood, soil, aquatic plants, or eucalyptus bark, to obtain salt (Oates 1978; Rode, Chapman, Chapman, et al. 2003; Rothman, Van Soest, and Pell 2006). Added salt demand under high-temperature conditions may be stressful to animals. In contrast to the situation where the climate gets hotter and drier, what happens when the climate gets wetter is not clear. Kibale National Park, Uganda, has experienced climate change well above the global average. The area receives 300 mm more rainfall per year than at the start of the century, and the average maximum monthly temperature has increased by 4.4 °C in the last 40 years (Rothman, Chapman, Struhsaker, et al. 2015). Corresponding with this change in climate, several tree species stopped fruiting (Chapman, Chapman, Struhsaker, et al. 2005), meaning that there was less fruit available for frugivores. For example, *Trilepisium madagascariense* (formerly *Bosqueia phoberos*) stopped fruiting at a site to the north of the park but continued to fruit at a drier site to the south; this has corresponded with a decline over time in blue monkey populations (*Cercopithecus mitis*) but not red tail monkey (*C. ascanius*) or mangabey populations (*Lophocebus albigena*; Chapman, Balcomb, et al. 2000; Chapman, Struhsaker, et al. 2010). Few studies have quantified changes in the quality of the leaves to test the generality of the greenhouse experiments because of the needed duration of monitoring. However, over the last 30 years, the quality of leaves eaten by some folivores has been described. In agreement with greenhouse experiments, Rothman, Chapman, Struhsaker, et al. (2015) show a general increase in fiber and a decline in protein in nonexperimental trees compared to data collected 15 and 30 years previously. Because many folivores select leaves with high protein-to-fiber ratios, declining leaf quality could have a major impact on folivore abundance. Based on the predictive model between colobine biomass and the protein-to-fiber ratio of mature leaves from common tree species in an area (Chapman, Chapman, Naughton-Treves, et al. 2004), a 31% decline in colobus monkey abundance would be predicted. However, this decline has not been seen, possibly because of a change in the composition of the old-growth forest at this site (Chapman, Struhsaker, et al. 2010; Gogarten, Jacob, et al. 2014), because the population can be flexible in what it eats, or because the decline may be yet to come. Not only may climate change affect fruiting periodicity, the composition of leaves, and what primates require in their foods; it also may change what is available for them to eat. Experiments suggest that the warming associated with climate change reduces plant diversity (Gedan and Bertness 2009), which could affect the foraging strategies and persistence of all primates. Climate change models have also predicted reduced diversity of fruiting angiosperms, which will reduce fruit availability for frugivorous primates (Vamosi and Wilson 2008). In addition to directly affecting species important in primate diets, climate change is expected to contribute to the increasing warming and aridification of the tropics and to interact synergistically with human-altered landscapes to reduce important wildlife habitat (Brodie, Post, and Laurance 2012).

BUSHMEAT HUNTING

Trends

To most primatologists, the bushmeat trade is undesirable and objectionable and should be stopped, but since it will not be stopped in the foreseeable future, it is something that nutritional ecologists must study to understand its consequences (R. D. Harrison 2011). Estimates of the extent of the trade are poor. However, E. Bennett et al. (2000) estimated that six million animals were hunted annually in Malaysian Borneo, which is approximately 36 animals per km², while in Africa, four

million metric tons of bushmeat were extracted each year from the Congo basin alone (Fa and Brown 2009). This trade means that even many national parks do not function as safe havens, and species in parks can still be driven to extinction through hunting (Oates, Abedi-Lartey, et al. 2000). In a global analysis of 60 parks, Laurance, Carolina Useche, et al. (2012) documented that researchers considered only approximately half of all reserves to have been effective over the last 20-30 years, while the remainder of the reserves had experienced an alarming erosion of biodiversity, which included a loss of primate species because of hunting (Oates, Abedi-Lartey, et al. 2000). This phenomenon is poignantly illustrated by a study in Tai: National Park, Cote d'Ivoire, where a park-wide survey illustrated that, regardless of primate species, density was 100 times higher near the protected research station and tourism site than in the remainder of the park (N'Goran et al. 2012). Ironically, reduced primate densities through hunting can, in the short term, lead to less competition for food, enabling animals to select the most nutritious foods. However, in the long term, the decrease in primate seed dispersers can lead to declines in primate food trees (Chapman and Onderdonk 1998; Peres and Dolman 2000). Hunters tend to target the larger primates, and evidence suggests that, with regard to forest-wide seed dispersal, removal of large-bodied primates is only partially offset by increases in smaller-bodied primates (Peres and Dolman 2000).

Predicted Responses of Primates with Different Foraging Strategies to Bushmeat Hunting

Managing wildlife populations for harvest has been a topic of inquiry for hundreds of years, dating back to the hunting reserves of kings (R. D. Harrison 2011) As a result, there is a wealth of information to predict the impact of hunting, which varies as a function of body size, life history, and diet (J. Lambert 1998; Leigh 1994a). This information has been refined to provide guidelines for sustainable hunting (Bodmer et al. 1997; Mayor et al. 2016), although we are unaware of any community of primates that are hunted sustainably. Given this wealth of data, we are not going to address this issue, except to state that hunters tend to target large-bodied animals (more value for the cost of the bullet and easier to transport per kg to market). This means that the hunted animals are often folivores, as large body size is a requirement of fiber digestion (McNab 2002), and these animals are often vulnerable because of their relatively large group size and sedentary lifestyle. Large-bodied folivores are particularly vulnerable because of their relatively slow life history. Some regions of South America are exceptions to this as folivore diversity is low, and hunters in some regions do not target howler monkeys (*Alouatta* spp.); however, hunting in other regions has caused local extinctions (Crockett 1998).

FUTURE DIRECTIONS

To guide future research, it is important not only to understand how the current situation is negatively affecting primates but also to identify positive trends that indicate opportunities for researchers and conservation biologists. Globally, there are two positive trends that offer opportunities for primate conservation : forest change trends and the formation of new protected areas. In most primate host countries, degraded forests now exceed the area covered by old-growth forests (FAO 2005). In fact, it is estimated that, in the 1990s, secondary forest replaced at least 1 of every 6 hectares of deforested old-growth forest (S. Wright and Muller-Landau 2006). Secondary forests now represent approximately 35% of all remaining tropical forests (Emrich et al. 2000). The year 2008 marked the first time more people lived in cities than in rural settings, and the rate of urbanization is increasing. The UN Population Division estimates that 90% of the world 's population growth between 2000 and 2030 will occur in cities in the developing world. Urbanization leads to declines in rural populations in many countries, particularly in those countries where the population growth rate has declined (A. Jacob et al. 2008; S. Wright and Muller-Landau 2006). Abandoned rural land offers great primate conservation opportunities because many of the plants that regenerate

earliest are palatable and nutritious and bear plentiful fruit. There are a variety of trajectories for future land use : abandoned land can be converted into huge agricultural monocultures, such as palm oil plantations (Linder2013), or to agroecosystems where primate conservation is possible to varying degrees (Estrada, Raboy, and Oliveira 2012), or to agricultural land with fragments and corridors (Pozo-Montuy et al. 2013). Alternatively, the land could be allowed to regenerate to natural forest, which offers greater potential for the persistence of primates. Baya and Storch (2010) surveyed a village site in Korup National Park, Cameroon, that was abandoned seven to eight years previously and found populations of all eight species of primates that occur in the region; in addition, sighting frequency was not significantly different from that in other sectors of the park surveyed in 2004-2005 (Linder 2008). In Kibale National Park, Uganda, seven years after an area of grassland was replanted with trees as part of a carbon offset program, all species of diurnal primates were present in high numbers, including the endangered red colobus and chimpanzee (Omeja, Lawes, et al. 2016; Omeja, Obua, et al. 2012). Regeneration in this area of Kibale National Park has been extensive (fig. 29.2), which offers hope for the future. In carbon offset projects, if primatologists know the nutritional requirements of endangered primates, they can guide what species are planted. Urbanization and abandoned rural land represent a significant opportunity, and we must proactively influence land use policy and manage these lands to make the largest conservation gains. A second positive trend is the continued formation of new protected areas. Since 1992, protected areas have grown steadily, increasing by an average of 2.5% in total area and 1.4% in number of sites annually (Butchart et al. 2010; Rands et al. 2010). By 2006, protected areas covered 24 million km², in 133,000 designated areas (Butchart et al. 2010 ; Rands et al. 2010). However, these positive developments need to be viewed from a balanced perspective (Andam et al. 2008; Joppa and Ffaff 2009 , 2010; Joppa et al. 2008). For example, it is estimated that 20 % of vertebrate taxa recognized as threatened by the IUCN do not live in protected areas (A. Rodrigues et al. 2004). Also, although protected areas are normally effective at protecting land from being cleared, they are less effective at eliminating logging, human-created fire, and bushmeat hunting (Bruner et al. 2001; Chapman and Peres 2001; Hartter et al. 2011; Oates 1996). Protected areas are also not necessarily effective at maintaining the processes that generate and maintain biodiversity (T. B. Smith et al. 1993). About one-half of all protected areas are experiencing an erosion of biodiversity (Laurance, Carolina Useche, et al. 2012). Also, it is estimated that more than two-thirds of critical sites for biodiversity have incomplete or no protection (Butchart et al. 2010). This means that local communities need to be meaningfully integrated into conservation efforts, so that some of their needs can be met and positive park-people relations can be achieved. Researching how to make the largest conservation gains for primates from existing and new conservation areas is a clear research priority and will involve working closely with the local communities.

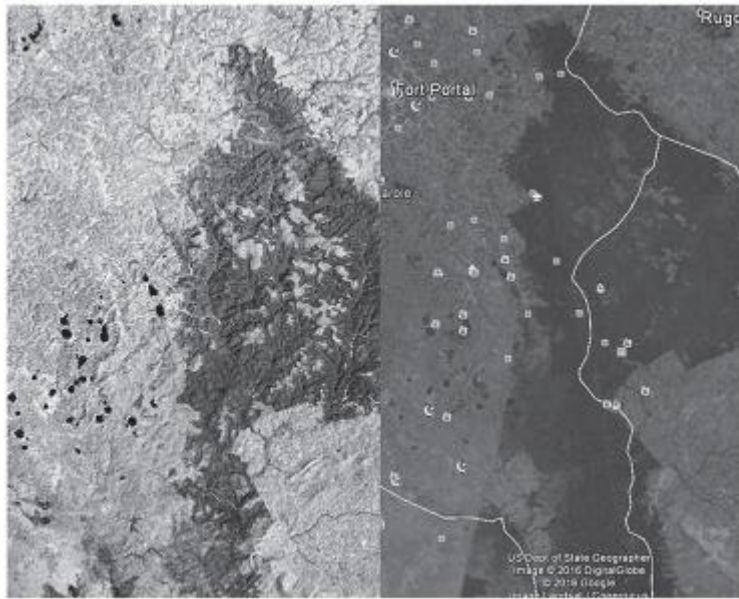


Figure 29.2. A satellite image of Kibale National Park, Uganda, in 1993 and a similar image taken from Google Earth in 2016 showing the extent of forest regeneration occurring in 23 years. The forested area is dark gray, and the agricultural and grazing land is light gray (the dark areas to the west of the park are crater lakes).

SUMMARY

Many primate populations are threatened as the result of human actions. We are now ethically obligated to take conservation action. To do this, conservation practitioners need to predict negative changes prior to their occurrence. In this chapter, we have used our knowledge of primate nutritional ecology and foraging strategies to make general predictions as to how primates could respond to three global threats : habitat destruction through logging and fragmentation, climate change, and bushmeat hunting. Logging and fragmentation have been extensive over the last few decades and are showing few signs of slowing down, except in areas where there is little or no forest left . In general, folivores typically do better in logged and fragmented areas than frugivores, but this is not always the case, and some frugivores can do well in these disturbed habitats. Climate change is altering the fruiting patterns of trees, creating periods of fruit scarcity, and decreasing the quality of leaf resources; these changes correspond to declines in insect abundance and lead to some forested areas currently supporting primates being unable to support closed-canopy forest. The bushmeat trade is a large industry that is decimating many primate populations. Hunters tend to target large-bodied animals, which means the hunted animals are often folivores, as large body size is a requirement of fiber digestion, and these animals are often vulnerable because of their relatively large group size and sedentary lifestyle. They can also unsustainably target large-bodied frugivores. Despite all the research on primate foraging and nutritional ecology published to date, we conclude that we have insufficient knowledge to predict how a particular species in a particular location will respond to disturbance. Thus, there are many ways that new academic studies can contribute to the future conservation of primates.

CONCLUSIONS

No matter what the nutritional needs of a species or how they meet those needs, from a conservation perspective, it is critical not to remove the food resources that meet those needs. It is a paradox that bushmeat hunting lowers primate population density, reduces competition, and thus increases the amount of food available per individual; thus, processes that have negative effects at a population level can be beneficial at an individual level. However, in no way can this be considered beneficial for a primate population. Primate species that have a flexible foraging strategy will be impacted less by forest degradation than those with a rigid foraging strategy or specific dietary needs; however, in general, at the present time, we have insufficient knowledge of nutritional

ecology to state a priori which species are flexible and which are not. It is our hope that we have illustrated the importance of maintaining forests and the food resources they contain and that this will provide researchers, conservation biologists, and managers motivation to maintain more forests, work on connecting fragments with corridors, provide guidance to restoration projects , and , in general, consider foraging needs whenever a forest is going to be altered.