
Review Article

What hope for African primate diversity?

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Abstract

Available empirical evidence suggests that many primate populations are increasingly threatened by anthropogenic actions and we present evidence to indicate that Africa is a continent of particular concern in terms of global primate conservation. We review the causes and consequences of decline in primate diversity in Africa and argue that the major causes of decline fall into four interrelated categories: deforestation, bushmeat harvest, disease and climate change. We go on to evaluate the rarity and distribution of species to identify those species that may be particularly vulnerable to threats and examine whether these species share any characteristic traits. Two factors are identified that suggest that our current evaluation of extinction risk may be overly optimistic; evidence suggests that the value of existing forest fragments may have been credited with greater conservation value in supporting primate populations than they actually have and it is clear that the extinction debt from historical deforestation has not been adequately considered. We use this evaluation to suggest what future actions will be advantageous to advance primate conservation in Africa and evaluate some very positive conservation gains that are currently occurring.

Introduction

Tropical countries harbouring primate populations are losing approximately 12.5 million hectares of forest

annually; an area just less than the size of the state of Florida or three times the size of Denmark (Chapman & Peres, 2001). Given that 90% of primate species worldwide are dependent on forest habitats (Mittermeier & Cheney, 1987) this figure is alarming to say the least. Indigenous forests are also being degraded by logging and forest fires (Nepstad *et al.*, 1999) and primate populations are being dramatically impacted by commercial and subsistence hunting (Fa *et al.*, 1995; Oates, 1996). Thus, the future for primates looks grim enough without considering the as yet largely unquantified and unknown impacts of global climate change on forest ecosystems (Taylor & Hamilton, 1994; Hengeveld, 1995; Hulme *et al.*, 1995; IPCC, 1996).

Africa is a continent of particular concern in terms of global primate conservation, for a variety of reasons. First, it harbours a high primate diversity – at least 64 species are recognized; fifteen prosimians, 46 monkeys, and three apes (IUCN, 1996), representing approximately 30% of extant primate species. Among fifteen countries worldwide scoring highest for primate species richness, nine are in Africa; including Democratic Republic of Congo (DRC), Cameroon, Nigeria, Peoples Republic of Congo, Equatorial Guinea, and Central African Republic (Cowlshaw & Dunbar, 2000). Second, historically African forests have been highly dynamic, experiencing several cycles of expansion and contraction and in many regions forests have persisted in fragmented form (Hamilton & Taylor, 1991). Large-scale, historical processes (e.g. speciation, extinction and dispersal) have been important in shaping the current patterns of primate distribution on the continent (Lawes & Eeley, 2000). Unlike South America and Asia, Africa is relatively dry; most of the rainforest is situated in a belt that extends <10° north and south of the equator and it is frequently broken by savanna or dry forest, such as the 300 km wide Dahomey Gap in West Africa. Thus, with the exception of the Congo Basin, African primates tend to occur in relatively small forest blocks and the majority of primates occupy relatively small geographical ranges (Eeley & Lawes, 1999; Cowlshaw & Dunbar, 2000). Third, many African countries have high human population growth rates, with each woman on the continent bearing on average five to seven children (United Nations Population Division, 2001). This is associated with some of the

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lowest per capita incomes in the world; most people living on <\$1 day⁻¹. Thus, people are often highly reliant on natural resources and population growth rate has been positively correlated with the rate of deforestation in West and Central Africa (Harcourt, 1995). Throughout the 1980s and into the 1990s high levels of foreign debt (a mean of 58% of sub-Saharan countries' Gross National Product and as high as 241%) placed strong pressures on governments to encourage timber harvesting and forest conversion (Stuart, Adams & Jenkins, 1990). While this situation is changing, many countries are still struggling to develop as quickly as possible and using natural resources is one quick means of reaching development goals. With this suite of circumstances it is perhaps not surprising, although no less shocking, that of the 64 species of nonhuman primates found in Africa, 25 are classified as 'at risk', ten (including the apes) as 'vulnerable' and two Scater's monkey (*Cercopithecus sclateri*) and the drill (*Mandrillus leucophaeus*), as 'endangered' (IUCN, 1996). Indeed, recent studies of declines in gorilla (*Gorilla gorilla*) and common chimpanzee (*Pan troglodytes*) populations have lead to a call for the status of both species to be upgraded from 'vulnerable' to 'critically endangered' (Walsh *et al.*, 2003).

We review the causes and consequences of decline in primate diversity in Africa. First we examine the major threats to African primate populations and illustrate why our understanding of the situation remains poor. We go on to identify those species that may be particularly vulnerable to threats and examine whether these species share any characteristic traits. Next we investigate the ability of primate populations to survive in an increasingly fragmented landscape. Finally, we ask whether it is already too late – is there an extinction debt from historical deforestation that is not being considered?

What are the main threats to African primate populations?

Africa is an immense continent covering approximately 30 million km² and encompassing 49 countries. It is not surprising, therefore, that the threats to Africa primate populations are many, varied and complex. One of the difficulties of defining categories of threat to primate populations is that threats are inevitably correlated. For example, while commercial logging may harvest relatively few trees (typically <10% of canopy trees), with varying affects on primate populations (Plumptre & Reynolds,

1994; Chapman *et al.*, 2000), the associated infrastructure development encourages immigration, which in turn increases the local human population, leading to increased agriculture, hunting pressure and further deforestation (Oates, 1996); all with strong negative effects on primate populations. For example, certain areas of Taï National Park, Côte d'Ivoire, have come under heavy pressure from new settlers. In 1972 the human population density surrounding Taï was estimated at 1.3 individuals ha⁻¹ (Martin, 1991). Since then timber exploitation has opened up large areas neighbouring the park for agriculture and farmers from the Sahel region have immigrated into the area. In 8 years the human population density increased sixfold leading to increased encroachment and slash-and-burn activities in the park (Chapman *et al.*, 1999). Despite such correlations between potential threats it is nevertheless useful to categorize threats to primate populations as these help to define areas where conservation actions can be targeted. Below, we consider four main categories of threat to African primates: deforestation, bushmeat hunting, disease and climate change. However, while these categories of threats directly impact on primate populations, the ultimate factors that will dictate the future of primate conservation on the continent are political and economic stability (IUCN, 1996). Political instability is an increasing threat to the effective implementation of conservation programmes in Africa. For example, of 42 projects recommended by the IUCN/SSC Action Plan for Primate Conservation in 1986, roughly a quarter were disrupted by civil war and political instability in the next 10 years (IUCN, 1996; Hart & Hart, 2003).

Deforestation

Prior to clearing and habitat alteration by people, the rainforests of Africa covered an estimated 3,620,000 km²: 74% of which was found in Central Africa, 19% in West Africa, and 7% in East Africa (Martin, 1991). While estimates vary, it is clear that forest area has been drastically reduced and up to two-thirds of the original forest area has now disappeared. For example, the FAO (1993) estimates that in 1985 Central African forests included some 1,717,450 km², while West African forest encompassed 143,260 km², and East African forest only 30,000 km². According to Martin (1991) the amount of forest remaining compared with its original extent is approximately 1,490,000 km² or 55% in Central Africa, 190,000 km² or 28% in West Africa and 70,000 km² or

28% in East Africa. Between 1981 and 1990, key countries supporting high primate population density experienced an annual deforestation rate of 0.16 to 0.92%; in most more than half of the original forest may have disappeared and in some, such as Nigeria and Uganda, <5% of the original forest cover is now thought to remain (Cowlshaw & Dunbar, 2000). Recent assessments suggest that African forests are currently being converted at a rate of 0.4 to 0.5% per year (Mayaux *et al.*, 2005). The figures are alarming and suggest that the protection and proper management of remaining forests, particularly in East and West Africa, is a high priority.

The primary causes of deforestation are commercial logging and clearing for agriculture. Few studies have directly examined the impacts of commercial logging on primate communities in Africa and comparisons among those that have are limited because of the different methodologies used. Studies also vary with respect to the logging compartment size, extraction regimes and incidental damage levels, the original composition of the primate communities, proximity to undisturbed primary forest and the time between logging and the monitoring of the primate populations. In addition, improved access resulting from the logging operation may or may not have increased the synergistic effects of hunting. Such variability has led to different conclusions, even among study areas in close geographical proximity and among sites with similar primate species assemblages. For example, Chapman *et al.* (2000) censused primates in logged and unlogged areas of Kibale National Park, Uganda and found red colobus (*Piliocolobus tephrosceles*), blue monkeys (*Cercopithecus mitis*), redtail monkeys (*C. ascanius*) and grey-cheeked mangabeys (*Lophocebus albigena*) were all negatively affected by logging, but black-and-white colobus (*Colobus guereza*) appeared to do well in some disturbed habitats. In contrast, just a few 100 km away in Budongo Forest Reserve, Plumtre & Reynolds (1994) found that black-and-white colobus, blue monkeys and redtails were more abundant in logged than in unlogged areas.

There is clearly still a lot to learn about the effects of commercial logging on primate communities. However, while responses to logging are highly species and locality specific, it appears that the extent of disruption of the forest canopy and removal of important food trees are critical factors. For example, no significant difference was observed in black colobus (*Colobus satanas*) populations of logged and unlogged forests at Lopé Reserve, Gabon, where the rate of extraction was very low (1–2 trees ha⁻¹) and there

was no major change in the forest composition and structure (Brugière, 1998). While in Kibale Forest, Uganda of the nine species that contributed more than 95% of the harvest volume, all were red colobus food trees and there was a significant decline in red colobus densities in the logged area (Struhsaker, 1997; Chapman *et al.*, 2000). At Budongo Forest, Uganda, populations of blue monkeys, redtails and black-and-white colobus showed no significant change between 1992 and 1996 under low levels of extraction, mainly because only mahoganies, which are not an important primates food trees, were removed. However, in one sawmill concession where *Cynometra* was felled and damage levels were higher, both blue monkeys and black-and-white colobus declined in density (Plumtre & Johns, 2001).

Small-scale, shifting agriculture (slash-and-burn agriculture) and the collection of natural resources by rural populations also play a significant role in the loss and degradation of forest habitats, although to date perhaps they have not received sufficient attention. Archaeological and palynological evidence suggests that forest clearance for agriculture may have had a profound impact on tropical rainforest habitats in Africa for a long time and especially in the last 1000–2000 years (Tutin & White, 1999). In the Congo Basin there is evidence that from about 2400 years ago people were collecting fruit and nuts, hunting primates (including chimpanzees and gorillas) and using fire to clear large areas for agriculture and growing oil palm (*Elaeis guineensis*; Tutin & White, 1999). At low densities, shifting agriculture probably contributes little to deforestation, but increasing population pressures, shorter and less frequent periods of fallow and inappropriate agricultural methods have made subsistence shifting agriculture a major cause of tropical forest loss in recent years (Cowlshaw & Dunbar, 2000). Where population pressures are particularly high, such as the eastern DRC, impacts on forest habitat may be severe (Mayaux *et al.*, 2005). In the DRC it has been estimated that the volume of fuelwood harvested each year is 200 times greater than the volume of the commercial timber harvested (Leslie *et al.*, 2002). This sort of disturbance is regionally variable, but we know very little about how primates respond. Near Kibale forest in Uganda, Chapman *et al.* (2003) found that of sixteen forest fragments used by primates in 1995, three (19%) were cleared (mainly for fuelwood and charcoal production) to the extent that they were no longer occupied by 2000. Once cleared the patches were used for agriculture. Fimbel (1994) investigated

the relative value of young successional forest on abandoned agricultural land in Sierra Leone and found that while the abundance of primates was higher in old growth forest, animals did frequently use the successional forest. This suggests that the mosaic of abandoned agricultural land, secondary and old growth forest, that characterizes much of Africa's rural landscapes, can be of value to conservation. However, any metapopulation management strategy should be used with great caution as we lack sufficient information on what area of old growth forest is needed as a source to ensure the persistence of a variety of primates, and would need to take into account additional factors such as whether or not local agriculturalists also hunt primates.

Bushmeat hunting

Subsistence and commercial hunting are having devastating impacts on primate populations in many regions in Africa, even in protected areas (Peres, 1990; Redford, 1992; Wilkie, Sidle & Boundzanga, 1992; Bowen-Jones & Pendry, 1999). From case studies, it is clear that bushmeat hunting provides a major source of food for many local communities and primates are often the target of such hunting activities (Martin, 1983; Fa *et al.*, 1995; Fitzgibbon, Mogaka & Fanshawe, 1995). Compared with many other taxa, primates are relatively large bodied, giving a good return of meat for hunting investment, most also live in groups and are diurnal and relatively conspicuous, and some are terrestrial, making them a sought after prey and they are considered highly palatable (Struhsaker, 1999). In an extensive survey across west and central Africa, primates contributed 12.0% of all hunted animals (Fa, Ryan & Bell, 2005). The figures are alarming. For example, in the 372 km² Arabuko-Sokoke Forest in Kenya, 1202 blue monkeys and 683 yellow baboons (*Papio cynocephalus*) were killed by subsistence hunters in 1 year, a number far above sustainable harvest levels (Fitzgibbon *et al.*, 1995; Fitzgibbon, Mogaka & Fanshawe, 2000). Hunting, exacerbated by the opening up of forest areas although logging and the growth of local human populations, has been identified as the primary cause in the near extinction of Miss Waldron's red colobus (*Procolobus badius waldroni*) in West Africa (Oates *et al.*, 2000), of which only a few remnant populations remain (McGraw, 2005). Problems may also be exacerbated where people have migrated into new areas, causing a breakdown in traditional practices. For example, in the Arabuko-Sokoke Forest, Kenya, the

indigenous Sanya people were traditionally hunter-gatherers who never hunted primates, while the Mijikenda people, who arrived in the early 1900s, are subsistence farmers who hunt a wide range of species including baboons and blue monkeys (Fitzgibbon *et al.*, 2000).

The Congo Basin is the biggest centre for bushmeat hunting worldwide and in many areas, particularly in central Africa, bushmeat makes up 80% of people's protein intake (Pearce, 2005). While the local demand for and consumption of bushmeat remains high, for example in the DRC 57.1% of the primates harvested are eaten in the villages and do not make it to the market (Lahm, 1993), the extent and intensity of commercial hunting has increased dramatically over the past decade (Wilkie *et al.*, 1992; Oates, 1996; Bowen-Jones & Pendry, 1999; Auzel & Wilkie, 2000). Martin (1983) found that in Nigeria 50% of the human population ate bushmeat regularly and bushmeat was popular with all income groups. Bushmeat is even becoming fashionable in Europe (Pearce, 2005). In many areas, hunting has shifted from a primarily subsistence activity to an organized, commercial venture. A market survey in two cities in Equatorial Guinea with a combined population size of 107,000, recorded 4222 primate carcasses being brought to market in 424 days (Fa *et al.*, 1995). Yet as dramatic as these figures appear, they likely represent an underestimate of the actual impact of bushmeat hunting on primate populations. Harvest estimates mostly come from market surveys and do not include primates that are consumed in villages. Furthermore, interview results are generally biased and underestimated because hunting is officially prohibited in many areas where it occurs (Johnson, 1996; Bowen-Jones & Pendry, 1999). Regardless of this it is clear that primates are being hunted in great numbers and in an unsustainable fashion in many areas of Africa. Barnes (2002) warns that while we may now be seeing a bushmeat boom we will soon see a bushmeat bust. Modelling the effects of harvesting pressure he showed that large harvests can be obtained for many years, but that population collapse can happen quickly given growing hunting pressure in conjunction with shrinking habitats.

Disease

Disease and parasites pose significant conservation risks to primate populations, many of which are already threatened or endangered by habitat loss and/or hunting (Wallis & Lee, 1999). A dramatic example are the

outbreaks of the Ebola virus that have contributed to the reduction of gorilla and chimpanzee populations by more than 50% over a broad geographic range in western equatorial Africa between 1983 and 2000 (Walsh *et al.*, 2003; Leroy *et al.*, 2004). In the Tai National Park, Ivory Coast, the recent deaths of at least six chimpanzees were attributed to anthrax, a disease not previously known to occur in tropical forest (Leendertz *et al.*, 2004). Polio epidemics too have caused widespread mortality in wild chimpanzee communities (Goodall, 1986). There are many examples. Cheney *et al.* (1988) found that illness accounted for more deaths than predation in one troop of vervet monkeys (*Cercopithecus aethiops*). Brain & Bohrman (1992) found Chacma baboons (*Papio ursinus*) living in the Namib Desert were heavily infected by ticks and speculated that these infections were responsible for more than half (n = 18) of recorded infant deaths.

The threat to primate populations from disease and parasites cannot be taken lightly and such risks are likely to increase in the future as humans continue to encroach upon nonhuman primate habitats. Recent investigations in Uganda have demonstrated that various forms of anthropogenic disturbance alter the dynamics of parasite infection in primate populations (Chapman, Gillespie & Goldberg 2005a). Among red-tail monkeys, for example, the prevalence and richness of gastrointestinal parasite infections were greater in logged than in undisturbed forest (Gillespie, Chapman & Greiner, 2005). Black-and-white and red colobus from forest fragmentation had increased parasite prevalence compared with populations in undisturbed forest (Gillespie & Chapman, 2006) and infection levels were strongly influenced by host density (Chapman, Speirs & Gillespie, 2005b). Finally, a study comparing parasite infection among colobus populations living at the forest edge and in the interior found that the proportion of individuals with multiple infections was greater in edge (Chapman *et al.*, 2005c) and the prevalence of specific parasites also varied between groups. For example, *Oesophagostomum* sp., a potentially debilitating parasite, was 7.4 times more prevalent among edge-dwelling red colobus than in animals inhabiting the forest interior.

Evidence that some conservation actions may actually endanger primate populations by promoting disease transmission is also alarming. As conservation agencies in Africa increasingly turn to ecotourism as a strategy to provide local communities with benefits from protected areas (Struhsaker, Struhsaker & Siex, 2005), and as the number of forest research sites increase, so does the pos-

sibility of disease transmission via these activities. Already, a number of cases have been documented of primates in ecotourism and/or research sites contracting infections with likely human origins. For example, in 1966 six chimpanzees at Gombe National Park, Tanzania, died from a polio-like virus and six others were paralyzed for life (Goodall, 1986; Wallis & Lee, 1999). In 1996, a severe skin disease was documented among gorillas at Bwindi Impenetrable National Park, Uganda and skin biopsy confirmed the presence of scabies (Wallis & Lee, 1999).

Climate change

There is growing appreciation at the academic and policy level of the potential scale of the effect that climate change could have on African biodiversity (Hannah *et al.*, 2002; Lovett, Barnard & Midgley, 2005a; Lovett, Midgley & Barnard, 2005b; McClean *et al.*, 2005). Some estimates suggest that this century the climate could warm by up to 5.8°C (IPCC, 2001). Future climate change predictions by the Intergovernmental Panel on Climate Change also suggest that Africa is the continent most vulnerable to change (IPCC, 2001; Lovett *et al.*, 2005b). As well as temperature changes, biodiversity will have to cope with changing rainfall patterns, declining water balances, increased extreme climatic events and changes in oscillations such as El Niño (Hannah *et al.*, 2002). Already, there have been numerous documented cases of shifts in the distribution, population abundance, life history and even survival of species in response to climate change (Pounds, Fogden & Campbell, 1999; Hannah *et al.*, 2002; Parmesan & Yohe, 2003). With primate populations increasingly isolated in protected areas surrounded by agricultural land that often supports high human densities, the loss of habitat as climate changes is of obvious concern. The flexibility of plant and animal populations to respond to future climate change by movement across the landscape is today constrained by human habitation and agriculture in the matrix. This is particularly an issue where primates occur in high elevation regions, such as those found in East and Central African reserves (e.g. Nyungwe, Bwindi and Mgahinga National Parks). Many of these are endemic species or sub-species with small geographical ranges and if climate change renders these areas unsuitable, the primates simply have no where to go and populations will become extinct (Eeley & Lawes, 1999). However, as far as we are aware, Dunbar's (1998) study of gelada baboons (*Theropithecus gelada*) is the only quantitative evaluation of

the potential effect of climate change on a primate species. Using a systems model of gelada socioecology, Dunbar (1998) suggested that the lower altitudinal limit of the species' would rise by approximately 500 m for every 2°C increase in global mean temperature, the land area available effectively halving and becoming more fragmented. A 7°C rise in temperature would be sufficient to reduce the species' total population size from its current size of approximately 250,000 to about 5000 and to confine geladas to a few isolated mountain peaks where their long-term persistence would be doubtful (Cowlshaw & Dunbar, 2000).

As well as direct effects of climate change on primate populations, primates may be affected by either the loss of particular plant species or changes in the phenological cycles of plant communities. Through a series of modelling exercises, McClean *et al.* (2005) studied the impact of projected climate change on the distribution of 5197 African plant species. For 81–97% of these species, areas of suitable climate are projected to decrease in size and/or shift in location, many to high altitudes and 25–41% of species will lose all their area by 2085. The models suggest dramatic changes in the Guineo-Congolian region, which today encompasses some of the most extensive blocks of remaining forest in Africa. Between 1970 and 2002 Chapman *et al.* (2004b) studied the phenological pattern of tropical trees that were important to primates in Kibale National Park, Uganda. This region today receives approximately 300 mm more rainfall per annum than it did at the start of the century, droughts are less frequent, the onset of the rainy season is earlier and the average maximum monthly temperature is 3.5°C hotter than it was 25 years ago; changes much higher than the global averages. At the community level, the proportion of trees fruiting decreased from the early 70s through the 80s, but rose between 1990 and 2002. Examining particular species over the whole period revealed a variety of patterns. For example, *Pouteria altissima*, a previously important primate food, exhibited a relatively regular pattern of fruiting during the 1970s, but rarely fruited in the 1990s. The results suggest that species level responses to climate change are likely to be complex and variable, and that for some tree species current conditions appear unsuitable for fruiting. It is also possible that changes in fruiting patterns are responsible for progressive declines in some primate species, such as blue monkeys, in the pristine sections of the park (Chapman *et al.*, 2000); however this speculation requires further and longitudinal study.

Which African primates are most vulnerable to threats?

Species that are rare, either in terms of their distribution or population density, generally face a greater extinction risk than more abundant species (Gaston, 1994). This is because small populations are more likely to die out than large ones, for example through demographic stochasticity, local catastrophes and slow rates of adaptation (Purves *et al.*, 2000). Examining the threat status of thirteen rare (range-restricted) African primates identified by Eeley & Lawes (1999), none is regarded as 'low risk', five species are classified as 'at risk', seven species as 'vulnerable' and one, the drill as 'endangered' (IUCN, 1996). However, as occupying a small range is one of the measures of threat used in this classification of threat status, this is perhaps unsurprising. In a systematic analysis that avoided such circularity and controlled for phylogenetic nonindependence, Purves *et al.* (2000) demonstrated that geographical range size is indeed significantly associated with high extinction risk in declining species of primates. Understanding the biogeography and characteristics of range-restricted species is therefore of value when considering the conservation status of African primates (Eeley & Lawes, 1999; Lawes & Eeley, 2000) and may help shed light on the threats to which they are vulnerable.

In fact, the majority of African primates occupy relatively small geographical ranges and only a few are widely distributed (Eeley & Lawes, 1999; Cowlshaw & Dunbar, 2000). In this they follow a general macroecological pattern that has been observed across a variety of taxa (Brown, Stevens & Kaufman, 1996) and which primates as a whole obey (Cowlshaw & Dunbar, 2000). Most of these range-restricted species are found in the species rich, forested regions of Central and West Africa (Figs 1 and 2; Eeley & Lawes, 1999; Cowlshaw & Dunbar, 2000). The primate communities of western equatorial Africa and Eastern DRC, for example, have been recognized as particularly species rich, with the former comprising at least 20 species (IUCN, 1996; Chapman *et al.*, 1999) and the high level of endemism in this area (Grubb, 1990; Kingdon, 1990; IUCN, 1996). The concentration of range-restricted species in these regions has resulted from a combination of evolutionary processes acting within the framework of forest expansion and contraction associated with glacial/interglacial cycles (Hamilton, 1988; Eeley & Lawes, 1999; Cowlshaw & Dunbar, 2000; Lawes & Eeley, 2000), and the influence of contemporary physical barriers, particu-

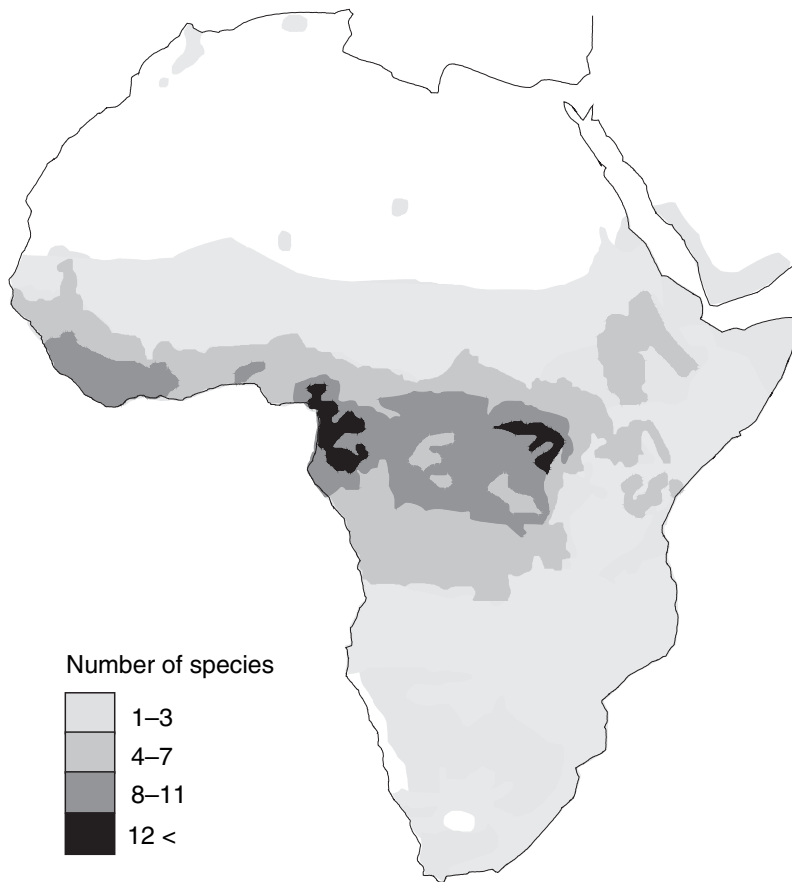


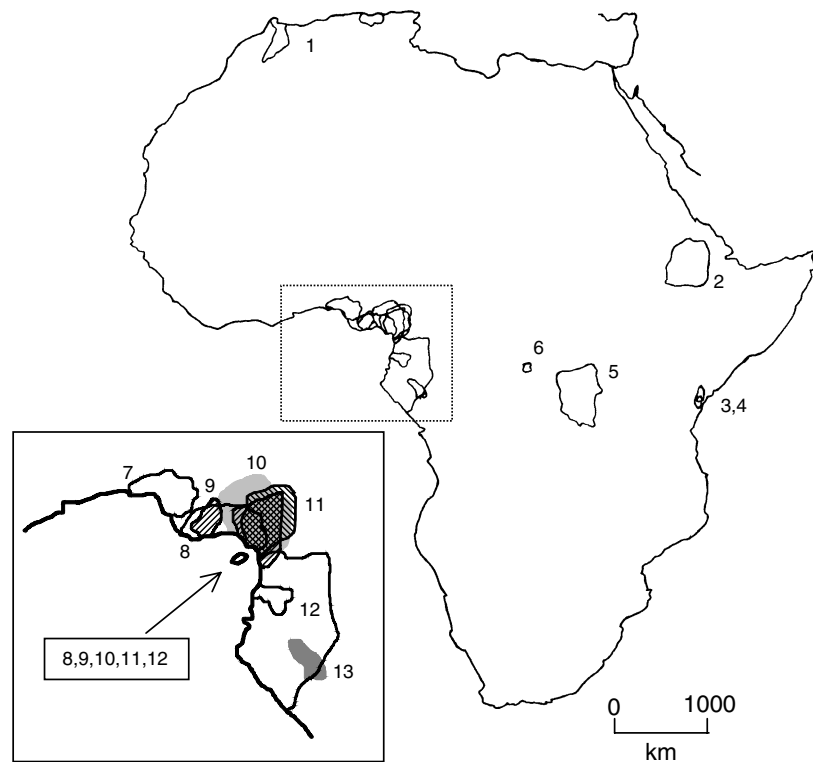
Fig 1 The distribution of anthropoid species richness across Africa (after Wolfheim, 1983; Lernould, 1988). Species richness is concentrated in the forested central and western equatorial regions, and gradients of richness are steepest in the vicinity of elevational barriers. (Figures 1–4 from Eeley & Lawes, 1999, copyright notice and Cambridge University Press, reproduced with permission)

larly rivers, oceans, mountain ranges, which limit dispersal and range expansion and restrict gene flow between populations (Chapman *et al.*, 1999; Cowlshaw & Dunbar, 2000). As restricted-range species tend to be clustered, any disturbance to the regions they inhabit is likely to threaten a relatively large number of species. As we have already observed, the major threats to primates in Central and West Africa include loss of habitat, disease, and bushmeat hunting, all of which have the potential to encompass the whole range of range-restricted species. For example, Sclater's monkey, one of the most restricted and rare primates in Africa, is suffering important habitat disturbance and widespread hunting pressure across its range in Nigeria (Ukizintambara & Thébaud, 2002). Most rare species live in countries that are being intensively deforested (i.e. >0.7%, the average rate of deforestation per annum in sub-Saharan Africa) and have few protected areas. Ukizintambara & Thébaud (2002) predict that the suitable habitat for most restricted *Cercopithecus* species will have disappeared within 300 years in West Africa,

630 years in Central Africa, 750 years in East Africa and 625 years in Southern Africa, and possibly much more quickly. It is worth noting that restricted-range species that are found in only a single country, such as the bonobo (*Pan paniscus*; DRC), sun-tailed monkey (*Cercopithecus solatus*; Gabon), dryas monkey (*C. dryas*; DRC) and Sclater's monkey (Nigeria) are particularly vulnerable also to political instability, including warfare (Wright & Jernvall, 1999).

Wider ranging species tend to be found outside the forest biome in woodland and savanna habitats, in areas of lower species richness. For example, among African catarrhine primates the average range size of species primarily occupying nonforest habitats is approximately five times that of forest dwelling species (Eeley & Lawes, 1999). These species tend to be less vulnerable. There tend to be more and larger national parks and reserves in savanna or grassland biomes, particularly in eastern and southern Africa, and many of these have been established for a long time, so more populations of these relatively widespread species are

Fig 2 The distribution of microareal anthropoids in Africa, i.e. those comprising the lowest quartile range size of the 51 species recognized (Rapoport, 1982; after Wolfheim, 1983; Lernould, 1988). Microareal species are found in association with areas of high relief, and cluster in western equatorial Africa where the Adamawa Highlands lie in close juxtaposition with coastal and riverine barriers. This region is one of marked endemism, characterized both by high species richness and, on average, low range size, and influences broad-scale biogeographical patterns in Africa. Species labelled: (1) *Macaca sylvanus*, (2) *Theropithecus gelada*, (3) *Cercocebus galeritus*, (4) *Procolobus ruformitratus*, (5) *Cercopithecus hamlyni*, (6) *C. salongo*, (7) *C. erythrogaster*, (8) *Procolobus preussi*, (9) *Cercopithecus erythrotis*, (10) *Mandrillus leucophaeus*, (11) *Cercopithecus preussi*, (12) *Colobus satanas*, (13) *Cercopithecus solatus*. (Reproduced with permission from Eeley & Lawes, 1999)



likely to be protected. However, a few range-restricted species are found in more marginal areas where overall species richness is low. For example the Barbary macaque (*Macaca sylvanus*) and the gelada baboon, these tend to be paleoendemic species, the surviving members of previously widespread groups that are currently restricted to marginal locations (Eeley & Lawes, 1999). This might explain why hotspots of species richness do not always coincide with hotspots of range size rarity (Hacker, Cowlshaw & Williams, 1998). Like all range-restricted species they are vulnerable to habitat disturbance, but of particular concern here are those restricted range species that occupy mountain areas, or high latitude regions, where they may be particularly vulnerable to the impacts of climate change and shifting patterns of climatic and habitat suitability.

In general, species that are able to exploit a variety of resources (i.e. that have a broad ecological niche) are likely to become more widespread. Thus, wide-ranging species tend to be ecologically generalized while range restricted species are more specialized. Cowlshaw & Hacker (1997) have argued that adaptation to climatic variability is often important in explaining large ranges (see also Harcourt, 2000). However, tolerance of climatic variability is just one measure of niche breadth. Among African primates,

species range size has also been related to both habitat and dietary niche breadth (Eeley & Foley, 1999; Eeley & Lawes, 1999; Wright & Jernvall, 1999; Harcourt, 2000; Ukizintambara & Thébaud, 2002). Although, variation across populations may be important in defining niche breadth (Harcourt, Coppeto & Parks, 2005), there appears to be a genuine relationship between ecological specificity and distribution, and flexibility may be the key: widespread species tend to be more flexible in their response to the environment than are range-restricted species (Cowlshaw & Dunbar, 2000). The important point here is that their tendency to ecological specificity makes range-restricted species even more vulnerable to threats: because they are less flexible, they are less tolerant of habitat disturbance and less able to adapt to changes in habitat structure, than are more wide-ranging generalist species.

Species that occupy a broad niche and are geographically widespread also appear to maintain a higher abundance across their range than more specialized species. Thus, different measures of rarity appear to be linked: species that are rare in terms of their range area also tend to be rare in terms of their population size, again exacerbating their vulnerability to threats. In fact, the relationship between range size and abundance may be better

described as triangular; maximum density increases with increasing range size and, while there are no species that occupy a small range and have a high density, widespread species may occur at either high or low density (Fig. 3; Gaston, 1994; Brown, 1995). Eeley & Lawes (1999) found that among African anthropoids widespread species occur at both high and low densities, while species that occupy relatively small ranges occur at low densities (Fig. 4; see also Cowlshaw & Dunbar, 2000). Wright & Jernvall (1999) have pointed out that although most widespread species tend to be locally more abundant, those that are less abundant and patchily distributed, such as the mandrill are at risk. Associated with the relationship between range size and abundance is a complex relationship between range size and body size, mediated through energetic constraints and reinforced by the influence of body size on dispersal ability and the tendency for smaller species to be more specialized (Brown & Maurer, 1989; Gaston, 1990; Eeley & Lawes, 1999). Species occupying relatively small ranges tend to have a small body size, while widespread species may be either small or large (Fig. 3; Gaston, 1994). In other words, larger species tend to occupy larger areas, while small species may be either

widespread or relatively range restricted. Again the African anthropoid primates appear to support this pattern (Fig. 4; Eeley & Lawes, 1999), as do *Cercopithecus* primates (Ukizintambara & Thébaud, 2002). Eeley & Lawes (1999) speculated that in general, small-bodied, specialist species should occupy small ranges and occur at lower abundance, while small-bodied generalist species should be relatively abundant and occupy large ranges, and large-bodied species should be widespread and generalist, but occur at lower densities (Fig. 3). They found mixed support for this among African anthropoids: widespread species were on average more generalist than species occupying smaller ranges (particularly in terms of habitat niche breadth), while among wider-ranging species those which were generally more abundant were on average smaller than those of low abundance (Fig. 4). Unexpectedly, however, species occupying small ranges at low abundance were on average the largest in terms of their body size. While this category did include several relatively small species, average body size was increased by the presence in this group of species such as the Barbary macaque, gelada baboon and gorilla. These larger bodied species with small ranges and low density are of particular concern as large

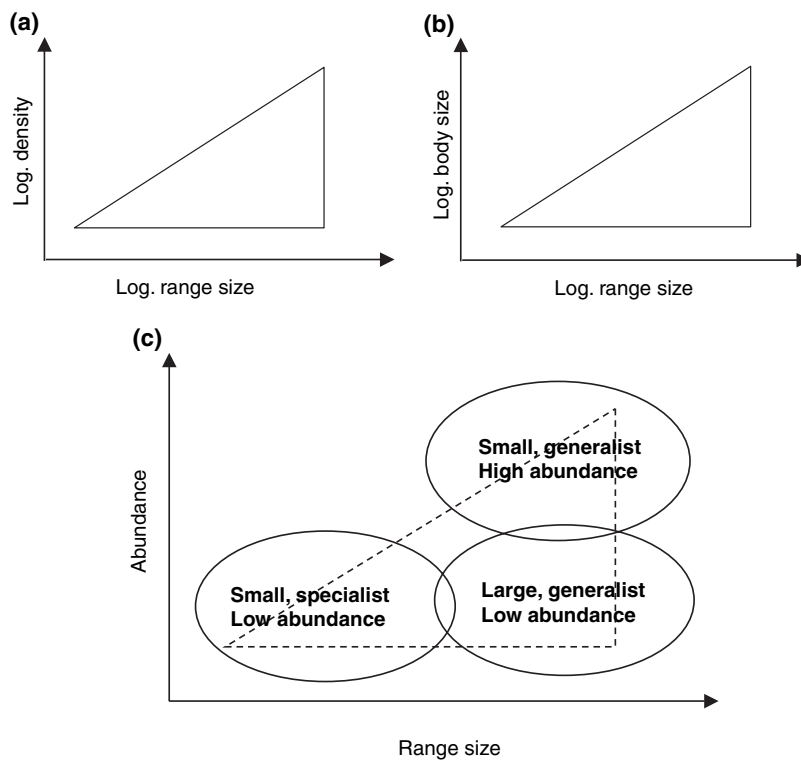


Fig 3 The general, theoretical relationship between species range size and (a) abundance (density), (b) body size (after Gaston, 1994); (c) combines these two relationships with the general positive correlation between range size and niche breadth, to identify some expected species characteristics in relation to range size. (Reproduced with permission from Eeley & Lawes, 1999)

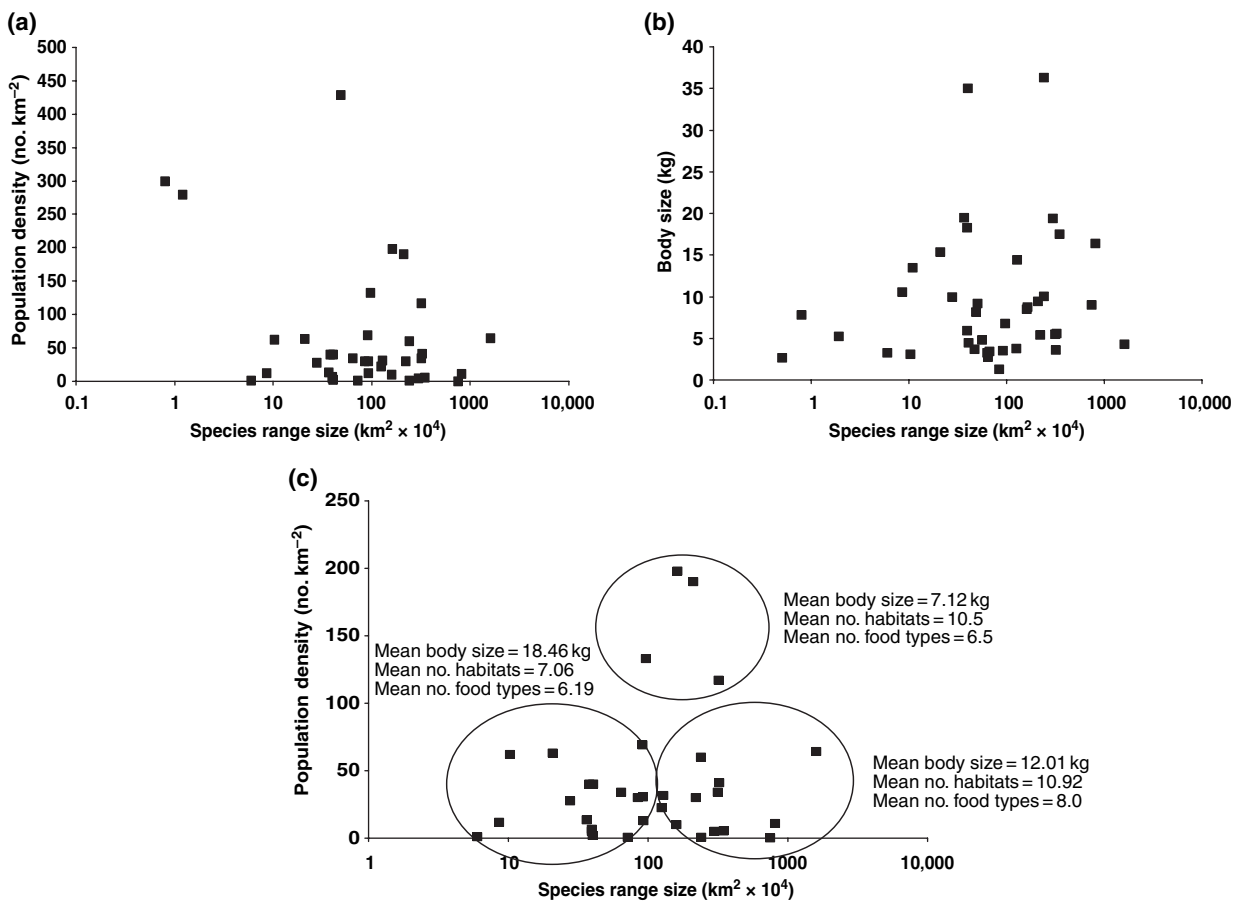


Fig 4 Among African anthropoids there is a triangular relationship between species range size and both (a) abundance, measured as population density ($n = 34$) and (b) body size ($n = 40$). Species occupying small ranges have a low abundance, while widespread species exist at both high and low density (the three outliers are the Tana River mangabey, *Cercocebus galeritus*, the Tana River red colobus, *Procolobus ruformitratus* and the red colobus, *Procolobus badius*). Small species occupy either small or large ranges, while larger species tend to be widespread. The first relationship is redrawn (c) with the three outliers removed to show how species habitat and dietary niche breadth characteristics vary with these relationships and the expected pattern identified in Fig. 3. (Reproduced with permission from Eeley & Lawes, 1999)

body size correlates with many extinction promoting traits, such as slower life histories, long inter-birth intervals and limited lifetime reproductive effort (Brown & Maurer, 1989; Wright & Jernvall, 1999; Purves *et al.*, 2000).

Isaac & Cowlshaw (2004) have recently demonstrated that species' biology underpins much of the variation in species vulnerability to extinction risk. Investigating the vulnerability of primate species to selective logging, agriculture and hunting, they found that primate species that are vulnerable to one form of threat are not more likely to be vulnerable to other threats, although selective logging and agriculture are both forms of habitat disturbance. As

different biological traits are correlated with each threat specific response, it implies different mechanisms of decline are associated with each threat type. Primates that exhibit a low ecological flexibility, live in a relatively narrow temperature range, tended to be more vulnerable to selective logging, as logged forests get hotter during the day and colder at night than do unlogged forests. In contrast, canopy-dwelling species that eat a low fruit diet tended to be more vulnerable to agriculture than terrestrial, frugivorous species, as shifting agriculture typically disrupts the canopy but cultivators actively retain the fruit trees. Larger species tended to be more vulnerable to

hunting as they are more attractive to hunters, providing a better return on investment than smaller species. Oates (1996) has suggested that folivorous species, such as red colobus, may be particularly susceptible to hunting because they occur in large groups, are relatively slow moving, highly vocal, and relatively conspicuous. On the other hand, frugivorous species may be vulnerable to hunting because their dependence on fruiting trees makes their ranging behaviour more predictable, while terrestrial species can be targeted with snares (Isaac & Cowlishaw, 2004). Nocturnal species tend to be less endangered than diurnal species because they are smaller, more faunivorous and less vulnerable to hunting (Wright & Jernvall, 1999).

Dietary preferences also influence species' vulnerability to habitat disturbance. Small, frugivorous primates appear to be more tolerant of selective logging provided levels of damage do not change the structure of forest or alter regeneration processes (Plumptre & Johns, 2001; but there are exceptions see Chapman *et al.*, 2000). On the other hand, some folivores may tolerate moderate disturbance as this may lead to a flush of leaf growth and increase the relative abundance of plant food species that limit populations during resource bottlenecks (Oates, 1996). Folivores may also be better able than frugivores to cope with a fragmented landscape. Several red colobus subspecies, for example, occur in small islands of East African forest, surrounded by dry woodland, savanna, or cultivated land, because they have the ability to survive for at least part of the year on a diet made up largely of leaves and can maintain higher population densities than more frugivorous species, allowing viable populations to persist for long periods (Oates, 1996; Onderdonk & Chapman 2000).

Thus, knowledge of a species basic biology can provide a prospective relative estimate of its vulnerability to extinction at least compared with related taxa. However, a word of warning is necessary. Although biological determinants of vulnerability to extinction can be identified, Purves *et al.* (2000) have also demonstrated how the severity of current anthropogenic pressures can overwhelm a species intrinsic resistance to extinction processes – several species are under more threat than expected and these generally occur in areas where forest losses are unusually high.

Can primates survive in an increasingly fragmented landscape?

With ongoing deforestation, agricultural expansion and climate change, primate populations are going to find their

forest habitats increasingly fragmented. Of concern is that existing forest fragments may have been credited with greater conservation value in supporting primate populations than they actually have (Thomas, 1994). In a recent review, Harcourt & Doherty (2005) estimated the minimum area requirements for primate species to survive exceed tens of square kilometre, but in Africa 65% of fragments studied were <1 km² (median size 0.2 km², n = 43). Therefore, most fragments are probably too small to support any primates over the long-term. For many species constrained in an increasingly fragmented landscape, the potential to exist in a metapopulation is often claimed to be their salvation. A metapopulation is a set of local populations within some larger area, where migration from one local population to at least some other populations is typically possible (Hanski & Simberlo, 1997). The dispersal of individuals across the landscape means that any empty habitat patches, resulting from the local extirpation of populations through stochastic fluctuations, may be recolonized from neighbouring patches. Although there have been few detailed studies of the ability of African primates to persist in metapopulations, those that have been conducted suggest that even species that appear to be suitable candidates do not always respond as expected. For example, across its range the blue monkey inhabits a variety of forested habitats much of which has been naturally fragmented during the last 100,000 years, and thus would appear to be well adapted to cope with anthropogenic fragmentation effects (Lawes, 2002). Yet in a series of studies of the samango monkey in South Africa, Lawes and co-workers have shown both that populations in small forest fragments are demographically vulnerable and also that they do not demonstrate a functional metapopulation (Lawes, Mealin & Piper, 2000). Nearly half (42%, n = 22) of the known populations of samango monkeys in KwaZulu-Natal Province occur in forests smaller than 500 ha (median = 470 ha, n = 54), which, given an estimated mean density of 0.59 individuals ha⁻¹ (Lawes, 1992), suggests many populations contain <150 reproducing individuals and their long-term viability is questionable. Although samango monkeys do use forest patches of varying size, the likelihood of occupancy decreases as forest area becomes small (<500 ha; Lawes, 2002). Using an incidence function approach to examine the occupancy of 199 forest patches, Lawes *et al.* (2000) found that samangos occupied only a few (7%), mainly large, forest patches and that the probability of patch occupancy did not vary with patch isolation, suggesting

that samango monkeys were unable to cross open areas between patches. Thus, if samango populations are extirpated from a forest patch it is unlikely that that patch will be recolonized. The processes that create empty habitat in the case of samango monkeys appear to be highly deterministic, area-dependent extirpation effects. Small samango monkey populations in small forest patches are demographically vulnerable (Swart, Lawes & Perrin, 1993) and small patches are seldom colonized. Samango monkey metapopulations if they exist at all are probably of the transient nonequilibrium, declining type characterized by local extinctions that occur in the course of a species decline to regional extinction.

In addition, the human use of forest fragments is often ignored. While studies of fragmented habitats in protected areas have provided important insights (Tutin, White & Mackanga-Missanzou, 1997), they may have biased our perception of the value of fragments to primates in general. In Africa, most forest fragments are not protected and are used by local landowners. Chapman *et al.* (2003) examined the survival of primate species in nineteen community owned forest fragments near Kibale forest, Uganda. In these forest fragments, black-and-white colobus experienced a 55% decline in numbers over 8 years (1995–2003), while the red colobus declined by 9% in 3 years (2000–2003) (Chapman *et al.*, 2004a; Chapman *et al.*, in press). The decline of colobus populations in this system of forest fragments could be largely attributed to their use by local communities. Forest fragments supported all the fuelwood needs of on average 32 people living in the immediate vicinity, and partially supported families up to three farms (approximately 400 m) away, representing 576 people. Intensive harvesting of fuelwood occurred when households were engaged in beer-brewing, gin-distilling, or charcoal production and once fragments were deforested they were used for agriculture (Onderdonk & Chapman, 2000; Naughton-Treves & Chapman, 2002; Chapman *et al.*, 2004a). Metapopulation theories are based on the idea that random fluctuations in local populations cause local extinctions and that unoccupied fragments are available for recolonization. At Kibale, this is not the case: extinctions appear to be driven by increased levels of deforestation that degrade the habitat and make it unsuitable for the primates. It appears from these studies that small and unprotected forest fragments face a bleak future; however, this is the reality of biodiversity conservation outside of protected areas in many areas of Africa. Habitat fragmentation clearly threatens the survival of primate populations.

Is it already too late for some species?

While the above evaluation of the status of primate populations is pessimistic, it is likely that it is not realistic enough. Until recently the extinction debt from historical deforestation has not been considered (Cowlshaw, 1999). Species-area theory predicts that as habitat area declines there will be a proportional drop in the number of species. Given the rate of global deforestation and the fact that primates appear to be particularly vulnerable to habitat loss, it is therefore surprising that so few species have gone extinct in recent years. Yet, in many cases extinctions take place some time after habitat loss occurs; this time lag is referred to as 'extinction debt'. Using species-area theory Cowlshaw (1999) examined extinction debt among African primates. He first demonstrated that primate species richness is strongly correlated with the extent of closed forest cover across African countries. He then used this relationship to predict the number of species that should have been lost, based on the documented reduction in forest cover. He estimated an average extinction debt of 30% of the national primate fauna (typically four to eight species) across many countries. Although these losses have yet to be observed, the lesson is salutary: without major conservation intervention it appears many species are on a trajectory to extinction. In many countries that have already experienced widespread deforestation many primate species may currently exist only by virtue of a time lag between initial habitat loss and eventual population extinction.

However, examples of population declines that represent losses because of extinction debt are rare because of the long time scale over which this process operates and a lack of long-term studies. One recently documented case may be that of the golden monkey (*C. mitis kandti*) in Mgahinga Gorilla National Park (MGNP), Uganda (Twinomugisha, Basuta & Chapman 2003; D. Twinomugisha and C.A. Chapman, unpubl. data). MGNP was declared a National Park in May 1991, before which it underwent a number of changes of name, status and management, affecting the conservation of the area. In 1991 the World Bank Global Environmental Facility established a trust fund to contribute to the park's conservation. Thus, with a more or less steadily rising level of protection and the potential for regeneration of degraded forest areas within the park, one would predict that the golden monkey population would increase. Yet, despite this improved protection, between 1989 and 2003 the relative density of golden monkeys

declined by approximately 80% (D. Twinomugisha and C.A. Chapman, unpubl. data). The distribution of golden monkeys has also changed, with groups now only being found in the most preferred habitat. It is possible that as the population density of golden monkeys has declined, animals are able to restrict their ranging to only the most preferred habitats. The decline of this endangered subspecies in an area that has received increased protection may represent an example of extinction debt about to be paid. The golden monkey has survived extensive habitat loss as the turn of the century and is now found only in a few national parks. For the population in the protected areas there was a time lag from when the habitat was lost to when the population collapsed. Whether the collapse will lead to extinction or simply a substantially reduced population size remains to be seen.

What hope for African primate diversity?

Primates are an integral part of the forest ecosystem: they comprise between 25 and 40% of the frugivore biomass in tropical forests (Chapman, 1995) and as seed dispersers and pollinators they play an important role in plant dynamics. Thus, primate conservation is clearly important. It is also clear that African tropical forests and the primate communities they support are seriously threatened. The near future could bring even greater potential for negative change, as a result of altered disease patterns and climate change. The correlation among many of these threats exacerbates their impacts. Our experience suggests that to advance conservation efforts for primates in Africa will require efforts on three fronts: political and socio-economic, adaptive management and research.

Africa is a continent of great political and economic instability and unless this is addressed there is little future for primate conservation in the region over the long-term. Studies have identified causal links between environmental degradation and violent civil strife, with the scarcity of natural resources fostering the emergence of conflicts (Dudley *et al.*, 2002). On the other hand, conflicts lead to increased pressure on natural resources and protected areas, often exacerbated by the presence of refugees and soldiers, as people's need for food and fuelwood and land for agriculture increases, and the trafficking of firearms adds to hunting pressures. At the same time, political unrest reduces the capacity to maintain and manage existing reserves as infrastructure and resources, including funding and personnel, decline. Perhaps more positively,

wars and civil unrest may hold back extractive industries, such as logging and mining. Recent examples of the negative effects that war has had on wildlife include massive declines in large mammals during the civil unrest in Uganda in the 1970s and 1980s (Dudley *et al.*, 2002), and declines in elephants and bonobos associated with civil unrest and human migration in the DRC (Plumptre *et al.*, 2000). Conservation programmes need to develop means of preparing for and dealing with such periods of civil unrest. Awareness is growing that political instability should not preclude conservation efforts from continuing (Draulans & Van Krunkelsven, 2002). Indeed, evidence from some areas, such as the Okapi Reserve, DRC, suggests that the single most important way to protect parks and reserves during periods of anarchy is by keeping engaged at all levels (Hart & Hart, 2003).

Also within the political/socio-economic realm, bushmeat hunting is clearly having a serious impact on primate populations across Africa. However, measures to mitigate the effects of the bushmeat trade will have to recognize its local, regional and national importance if they are to result in long-term conservation success (Bowen-Jones & Pendry, 1999). Across the continent, rural and urban populations still rely heavily on wild meat for protein, and the pressure will surely increase as the human population rises (Fa *et al.*, 2000; Fa, Currie & Meeuwig, 2003; Pearce, 2005). As well as being a personal necessity, bushmeat hunting provides an important source of revenue to local communities; for example, sales have been shown to represent 33% of total annual village income (Infield, 1988). The trade also makes a significant contribution to national economies. For example, in the Ivory Coast wild meat income is estimated at \$117 million, while in Liberia the total annual wild meat harvest is worth \$42 million (Fa *et al.*, 2000). It is clear that realistic alternatives, that provide food for people and an income for communities, need to be found if we are to stop the bushmeat crisis (Barnes, 2002; Fa *et al.*, 2003; Pearce, 2005).

The level of protection for primate communities within different regions is clearly limited and constantly changing. Within the countries of Africa with closed canopy forest, an average of 3.2% of each country's area is currently reserved in national parks or similar protected areas (Chapman *et al.*, 1999). The investment of different countries in national parks also is very dynamic; new parks are being created in some countries, while in others, parks are being heavily degraded or even degazetted. The reality is that conservation efforts on the scale needed are

very expensive. Currently, the operating costs of forested protected areas in Africa range from \$23 to \$208 km⁻² per annum, which is 1.4- to 11-fold lower than the costs of running protected areas in developed nations (Struhsaker *et al.*, 2005). This does not consider the costs of establishing new protected areas. Given the current economic situation in many countries in Africa and their level of foreign debt, this will require a substantial and sustained commitment on behalf of the international donor community.

Wildlife habitats in Africa experience extremely varied conditions in terms of their physical environment, cultural setting and human population density on their borders. As a result, it is necessary to take a variety of management approaches and these approaches will need to be adaptive (i.e. changing as the situation or our knowledge changes) and targeted at different time scales. It will typically not be appropriate to apply a successful approach developed for one location broadly to many other localities. This is illustrated by the lack of success of the application of community outreach strategies largely developed in South America to forested protected areas in Africa. Contrary to expectations, studies in Africa have demonstrated that none of the community outreach programs designed to promote positive community attitudes through education and financial benefits were correlated with forested protected area success (Struhsaker *et al.*, 2005). In fact, a study of protected areas in Uganda found that there was no evidence that such programs even promoted positive community attitudes towards parks (Mugisha, 2002). As Oates (1995, 1996, 1999) and others (e.g. Christensen, 2004) have pointed out, mixed development/conservation approaches, in which the conservation of wildlife and natural resources are regarded as part of a process of sustainable community development, are fraught with danger and require caution. If successful, attempts to bring development to people within or adjacent to a conservation area are likely to lead to increased migration into the region and because people rarely use natural resources in a sustainable way in the long run, the area is more likely to be devastated than conserved (Oates, 1996). In Nigeria, for example, multiple use forest management systems were overwhelmed by a lack of resources, poor management and corruption, resulting in the conversion of large portions of protected natural forest into permanent farmland (Oates, 1995).

Finally, more research is needed to guide effective conservation approaches. This is illustrated by a number of

scenarios we have already presented. For example, as recently as the 1980s the dominant perspective on prevention of infectious diseases was one of optimism (Cohen, 2000) and now it is considered one of the greatest risks to great ape populations. Similarly, we have little understanding of how many species will go extinct once the extinction debt is fully realized, or how much the climate will change in the next few decades and the consequences of these changes for primate populations. We need to concentrate conservation efforts in regions of high diversity and understand the threats to restricted range species so that we might better protect them in the long-term.

Although we have painted a fairly bleak picture, it is important to remain optimistic. There is still considerable potential for primate conservation in the forested regions of central Africa, in particular in the Congo Basin (Mayaux *et al.*, 2005). In other areas of Africa positive attitudes to conservation are increasing and this is being manifested in the creation of many new national parks. For example since 1993, Uganda had increased the amount of land protected as National Parks by 50%, so that now 4.7% of the country has the highest level of protected available under Ugandan law. Similarly, the government of Madagascar has announced that it will triple the size of its protected areas from 1.7 million to 6 million hectares between 2003 and 2008 (Ganzhorn, 2004; see also Gabon new parks system). Such efforts are clear reasons to be optimistic that present negative trends for primate conservation will be changed.

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