



Conservation of Red Colobus and Their Habitats

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A review of the conservation status of red colobus indicates that $\geq 38.9\%$ of the taxa are threatened with extinction in the near future. Although no taxon of red colobus appears to have gone extinct, many of their populations have. The major threats are hunting and habitat loss and degradation, but in some cases intrinsic biotic factors, such as predator-prey imbalance, are leading to serious declines in populations. I propose a general framework for evaluating conservation problems and possible solutions, with an emphasis on distinguishing between proximate and ultimate variables and the time scales involved. In general, most viable populations of red colobus occur in well-protected forests; usually national parks. I proffer recommendations to improve the conservation status of the parks, which will benefit red colobus and most other tropical forest species.

KEY WORDS: red colobus; conservation; park success; national park; habitat loss.

INTRODUCTION

The survival of Africa's red colobus (*Procolobus*), like many other nonhuman primates and medium to large-sized vertebrates of tropical rain forests, is threatened by hunting and habitat destruction. Crude estimates of the annual loss of natural tropical forest vary widely among countries, but in general it is *ca.* 0.7% for Africa and this rate appears to be increasing as the remaining area of forest decreases. The loss does not include the additional vast areas of forest that are degraded by exploitation. No African country has increased its forest cover (Struhsaker, 1997; WRI, 2000).

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The biodiversity losses due to habitat destruction and degradation are exacerbated by the ever-increasing levels of hunting in most parts of Africa (Robinson and Bennett, 2000). According to Conservation International (unpublished data), the numbers of primate species and subspecies threatened with extinction are estimated to be 47 (28%) for Africa, 72 (40%) for Asia, 68 (33%) for Central and South America, and 37 (54%) for Madagascar. These estimates are minimal because for a great many taxa of primates we lack sufficient information to determine their status. This erosion of primate diversity is one of the clearest indicators of tropical forest loss and degradation (Struhsaker, 1975, 1997; Johns and Skorupa, 1987; Chapman and Lambert, 2000; Waltert *et al.*, 2002).

Red colobus are good indicators of the overall health of Africa's rain forests because they seem particularly sensitive to habitat degradation (Struhsaker, 1975, 1997; Skorupa, 1986, 1988; Chapman and Lambert, 2000; Waltert *et al.*, 2002). They are also extremely vulnerable to hunting (Struhsaker, 1975, 1997, 1999; Martin and Asibey, 1979; Davies, 1987; Oates, 1996; Oates *et al.*, 2000; Waltert *et al.*, 2002) probably because they move in large noisy groups and because they seem less perceptive than the sympatric forest guenons. Even where they are hunted, red colobus are relatively easy to stalk and to observe (pers. observ.). Healthy populations of red colobus generally indicate healthy forest ecosystems.

I briefly summarize the conservation status of the various red colobus taxa for which there is information and identify the threats to them. I also present a conceptual framework and recommendations for conserving red colobus and their habitats.

Status of Red Colobus Taxa

The taxonomy of red colobus has been difficult to resolve, in part because none of the various taxa are sympatric. Two recent reviews of red colobus tentatively recognize 5 species and a total of 18 taxa (Grubb *et al.*, 2003 and Grubb *et al.*, in press). They are distributed across equatorial Africa from Senegal to Zanzibar and south to central Tanzania (Rahm, 1970; Kingdon, 1974, 2001; Struhsaker, 1975; Colyn, 1991).

The conservation status of most of these taxa is unknown. However, ≥ 6 are critically endangered, endangered or threatened with extinction and a seventh is virtually extinct. In other words, $\geq 38.9\%$ of the red colobus taxa are threatened with extinction in the near future. These are:

- 1) Miss Waldron's red colobus (*Procolobus badius waldroni*) has been eliminated over most of its range and may be extinct (Struhsaker, 1999; Oates *et al.*, 2000). Formerly living in western Ghana and

eastern Cote d'Ivoire, they appear to have been driven to virtual extinction by humans hunting for meat. Habitat loss and degradation have also contributed to their demise. Recent surveys in eastern Cote d'Ivoire recovered a tail and a complete and fresh skin from local hunters. The specimens are thought to be of *Procolobus badius waldroni*, suggesting that perhaps a few of them still remain (McGraw and Oates, 2002; McGraw (this volume)). However, even if a few survive, they are unlikely to represent a viable population.

- 2) The Niger Delta red colobus (*Procolobus pennantii epieni*) is a recently discovered taxon with a very restricted range within the Niger Delta of Nigeria. Its total population is apparently very small, fragmented and highly susceptible to hunting and habitat degradation (Grubb and Powell, 1999; Werre, 2000).
- 3) Preuss's red colobus (*Procolobus pennantii preussi*) occurs primarily, if not exclusively, in the Korup National Park and its perimeter in Cameroun with perhaps a small number residing in the adjacent Cross River National Park of Nigeria. They were more widespread in Cameroun during the past (Struhsaker, 1999). Napier (1985) listed 80 specimens collected in 1939 from Yabassi district. In 2000, monkeys that may have been red colobus of some sort were seen at the confluence of the Ndouo and Nkam Rivers west of Toumbassala in the Yabassi region of western Cameroun (Dowsett-Lemaire and Dowsett, 2001). Their very restricted range, combined with intense hunting pressure (Infield, 1988; Edwards, 1992; Dowsett-Lemaire and Dowsett, 2001) and logging (Waltert *et al.*, 2002) threatens their survival.
- 4) The Bioko red colobus (*Procolobus pennantii pennantii*) is now restricted to the southern one-quarter of the island of Bioko (Butynski and Koster, 1994), with a gross distributional range of <math><500\text{ km}^2</math>. There is no reliable estimate of the current total population, but they are threatened by increasing levels of hunting (Dr. Gail Hearn, pers. comm.) and forest loss and degradation (Butynski and Koster, 1994).
- 5) The Tana River red colobus (*Procolobus rufomitratu rufomitratu*) is restricted to very small, degraded, and highly fragmented forest patches along a narrow strip of the lower Tana River, Kenya. It is one of Africa's most endangered monkeys and may now number <math><1,500</math> (Butynski and Mwangi, 1995). The major threat to them is habitat loss due primarily to agricultural clearing and extraction of forest products (Butynski and Mwangi, 1995; Wiczowski and Mboru, 1999–2000; Mboru, 2003) and secondarily to alteration of river flow volume and cycles caused by hydroelectric power

dams upriver (Hughes, 1984). Less than 35% of the population is legally protected within the Tana River Primate Reserve, but even there the habitat is insecure because of inadequate law enforcement (Wieczkowski and Mbori, 1999–2000).

- 6) The Zanzibar red colobus (*Procolobus kirkii*) is essentially restricted to the southern half of Zanzibar (Unguja Island) and its numbers are estimated at $\leq 2,000$ by Struhsaker and Siex (1998; Siex, 2003). Although a few descendants of a translocation effort made in the mid 1970s may still persist near Ngezi on Pemba Island, they do not appear to be a viable population (Camperio Ciani *et al.*, 2001). Less than half of the taxon is legally protected within the small Jozani-Chwaka Bay National Park (about 60 km²) where the monkeys are reasonably secure. The majority of the species is threatened by habitat loss due to expanding agriculture and demands for firewood, charcoal, and building poles. Habitat loss is leading to population compression (Siex, 2003) and a likely decrease in geographical distribution. Hunting is a lesser threat, but some individuals are killed as perceived agricultural pests and, to a much lesser extent, for food (Struhsaker and Siex, 1998). Some are also killed each year by vehicles, though this has been greatly reduced by the installation of speed bumps at Jozani.
- 7) Bouvier's red colobus (*Procolobus pennantii bouvieri*) is known only from a very restricted area of the Republic of Congo, but no scientist has seen them for several decades and they may be extinct because of hunting (Oates, 1986–1990, 1996).

In addition to these 7 taxa, there are ≥ 4 others whose conservation status can be considered vulnerable:

- 1) *Procolobus badius badius* is restricted to Sierra Leone, Liberia and Cote d'Ivoire. The many years of civil war in the region have resulted in a breakdown of law and order and displacement of large numbers of people. All of these conditions are conducive to overexploitation of timber and bushmeat (Oates, 1999). The last stronghold of this taxon is likely to be the Tai National Park, Cote d'Ivoire, but even there poaching occurs at high levels and, given the current political instability of the country, the conservation status of Tai, the red colobus, and most other medium to large-sized vertebrates in the region must be considered vulnerable.
- 2) Thollon's red colobus (*Procolobus rufomitritus tholloni*) has a patchy distribution in the Democratic Republic of Congo (DRC), south of the Congo River in a block defined by the Congo, Kasai,

and Lomami Rivers. The population size of the taxon is unknown, but at least within the Lukuru area, and probably throughout most of their range, humans hunt them extensively. They are legally protected only in the Salonga National Park. Hunting pressure on them has likely increased wherever they occur due to the wars within DRC and the corresponding increase of weapons, ammunition, and people within their range (Thompson, 1999–2000).

- 3) The Uganda red colobus (*Procolobus rufomitratus tephrosceles*) occurs in a few isolated forests along the western side of Tanzania and in Kibale, Uganda. The largest and, perhaps, only viable population of the taxon lives in the Kibale Forest of Uganda. The forest is protected as a national park, it is reasonably large (766 km²), and hunting of primates by humans is essentially non-existent (Struhsaker, 1997).

Although crude estimates of the total population of red colobus in Kibale have been made (Struhsaker and Pope, 1991; Pope, 1995; Struhsaker, 1997; Chapman and Lambert, 2000), they are not particularly accurate because: a) only a relatively small proportion of the forest has been sampled; b) estimates of density based on line transects are problematic because of inherent difficulties, such as determining the area sampled and obtaining accurate group counts (Struhsaker, 1997; Mitani *et al.*, 2000); and c) group size varies tremendously within and between areas of Kibale (Struhsaker, 1975, 1997; Struhsaker and Leland, 1979; and Chapman *et al.*, 2002) thereby confounding the conversion of line-transect census data to accurate density estimates.

Approximately 60% of the Kibale park represents suitable habitat for red colobus and published density estimates for them range from 93 to 313 per km² (Struhsaker, 1997; Chapman and Lambert, 2000; Chapman *et al.*, 2002). However, there are parts of Kibale where red colobus are rarely, if ever, seen and density estimates have been made for only a very small percentage of the forest. In order to compensate for these uncertainties it is recommended that a much more conservative density estimate be assumed, i.e., 25–50 red colobus per km². When multiplied by the potential area of habitat (60% of 766 km² = 460 km²), these conservative density estimates indicate that there are $\geq 17,000$ red colobus in Kibale.

The Kibale park would appear to have a healthy and viable population, but long-term studies in two areas of the park indicate statistically significant declines in red colobus numbers. The clearest and most dramatic change has occurred in the Ngogo study area,

where census data spanning nearly 24 yr indicate a 43% decline in groups (Mitani *et al.*, 2000). Further study of the Ngogo population showed an even greater decline in red colobus over a 30-yr period (Dr. J. S. Lwanga pers. comm. and author's pers. observs.). Group size does not appear to have decreased, but the density of groups has (pers. observs.). The habitat at Ngogo is well protected and contains substantial areas of old-growth forest, so the decline is not obviously related to habitat degradation. Although several factors may account for the decline, predation by the unusually large community of chimpanzees at Ngogo most likely accounts for most of the change. Watts and Mitani (2002) estimated that at Ngogo chimpanzees killed 6.5–12% of the red colobus annually. This estimate of predatory impact is probably too low because the estimated population densities for red colobus that Watts and Mitani (2002) used were from an earlier period when red colobus were more abundant. Furthermore, because chimpanzees prey primarily on adult female and immature red colobus the impact of their predation is likely to increase exponentially because of the loss of breeding females and the greatly reduced recruitment of young colobus into the adult population.

A similar long-term study spanning 28 yr at the Kanyawara site of Kibale also indicated a 40% decline in red colobus numbers within old growth and protected forest, as well as in nearby selectively logged forest (Table 5 in Chapman *et al.*, 2000). The underlying cause of the decline in the red colobus population in the Kanyawara old-growth forest is less apparent. Although chimpanzees kill them there too, their impact does not appear to be as great.

Even though the Kibale park is relatively large and reasonably well protected, the declines in red colobus populations over the past 30 yr are cause for concern.

The *tephrosceles* red colobus in Gombe National Park, Tanzania also seem to have declined in numbers due to predation by chimpanzees. Stanford (1998) reported that red colobus group sizes have declined by nearly 50% over a 25-yr period and that 16–40% of them are killed each year by chimpanzees (Wrangham and Bergmann-Riss, 1990). The population appears to be seriously threatened with extinction because of predation by chimpanzees and because of the very small size (*ca.* 80 km²) and isolation of the Gombe park.

- 4) The Udzungwa red colobus (*Procolobus gordonorum*) is restricted to the fragmented forests of the Udzungwa Mountains and a few

isolated patches of forest in the nearby Kilombero Valley of south-central Tanzania. Although their total number is in the thousands, one published estimate of 15,400 (Dinesen *et al.*, 2001) is not well founded and is probably too high. The estimate is not based on systematic censuses or focal group studies, and it was extrapolated from small samples to enormous areas, including habitat that is unsuitable for red colobus. An earlier estimate by Rodgers and Homewood (1982) is 10,000 red colobus; however, they emphasized, that the largest single interbreeding population is certainly <2,000 individuals. We still lack a well-founded and reliable population estimate for them.

Recent studies indicate that group size and natality (number of infants per adult female) are adversely affected by forest degradation and small forest size. The largest groups with the highest levels of reproductive success live in large blocks of old growth, mixed evergreen and semi-deciduous forest (Struhsaker *et al.*, 2004). Correspondingly, attention must be given to conserving more of these forests within the range of *Procolobus gordonorum*.

At present, only about half of their range is protected within the Udzungwa Mountains National Park (UMNP). The remaining habitat is unprotected either on public land or in forest reserves that are not effectively protected. These forests are being degraded by logging, conversion to agriculture, collection of firewood, charcoal production, and hunting (Dinesen *et al.*, 2001; pers. observ.). The small forest remnants in the Kilombero Valley that contain red colobus and that lie outside the park are particularly vulnerable. For example, the Lukoga Forest was so seriously degraded by 1998 that forest regeneration seemed unlikely (Ehardt *et al.*, 1999). Similarly, the slightly larger Kalunga Forest Reserve was being totally destroyed because of lack of protection by the Tanzania Forest Department and local authorities charged with protecting it (Ehardt *et al.*, 1999; pers. observ. in 2003 and 2004).

A third forest in the Kilombero Valley, Magombera, was threatened with total destruction in 2002 when the Government of Tanzania agreed to relocate squatters there from the nearby Kilombero Sugar Estate. Fortunately, the international conservation community was alerted in enough time to launch an appeal to the Government of Tanzania that averted destruction of this forest, which contains >1,000 red colobus. It is hoped that the Government of Tanzania will soon annex the Magombera Forest to the adjacent Selous Game Reserve, which it declared it would do in 1980. Unless Magombera is legally added to the Selous and the forest

reserves—Udzungwa Scarp, Iyondo, Matundu, Ukami, Ndundulu, Nyumbanitu, and Nyanganje—in the Udzungwa Mountains are annexed to UMNP and given adequate protection, the red colobus and other forest-dependent species will suffer serious declines (Struhsaker *et al.*, 2004).

The only taxon of red colobus that is probably secure is *P. rufomitratu* *oustaleti* because it has an enormous range throughout the Democratic Republic of Congo, the Republic of Central Africa, and the Republic of Congo where there are still large areas of forest and low human population densities (Gautier-Hion *et al.*, 1999).

Summary of Threats

The major threats to red colobus monkeys throughout their range are hunting for meat by humans; habitat loss, degradation and fragmentation; and/or intrinsic biological problems. While the first 2 categories are obvious and well known, the third is one that is less commonly appreciated. Although I have highlighted the cases of predator-prey imbalance in Kibale and Gombe, other possible intrinsic biological threats to be considered include epidemics (e.g., possible herpes in *P.r. tephrosceles* [Struhsaker, 2000]) and reduced fecundity and survivorship due to overbrowsing of food resources resulting from population compression into small habitat Islands, e.g. in *Procolobus kirkii* (Siex, 2003).

A Conceptual Framework for Evaluating Problems and Developing Solutions

Although no taxon of red colobus appears to have gone extinct, most populations have. In general, the only viable populations of red colobus occur in well-protected national parks or reserves. Elsewhere they are gone or are rapidly disappearing. Without adequate protection of forests, red colobus and all other forest-dependent species will continue to decline. While there is no doubt that parks and other conservation areas form the critical foundation for any effective conservation program and, thereby, the effective conservation of red colobus and most other nonhuman primates, these protected areas face a wide array of problems. It takes much more than the legal acquisition and demarcation of land to effectively protect the resident flora and fauna.

The problems facing protected areas (PA) vary over time and space. Details of the problems and the status of a PA will depend on its

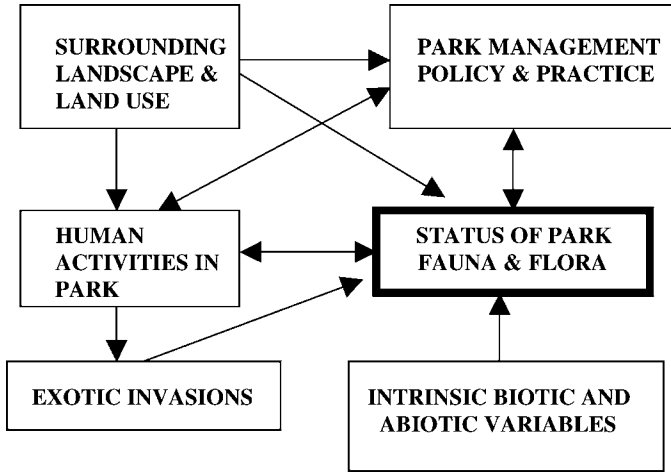


Fig. 1. Variables influencing the conservation status of protected areas and their interactions.

landscape setting, as well as PA management policy and practice (Fig. 1 and Struhsaker, 2002). In spite of this complexity, general guidelines can be developed that help to identify the problems and possible solutions. In one such attempt, Struhsaker (2002) classified 5 categories of problems according to whether they involved proximate or ultimate variables (Table I). Solving problems that involve proximate variables can be likened to the band-aid approach. In many cases the variables are given priority because they are apparent and because short-term results can sometimes be achieved quickly. This is important in terms of gaining more time to solve the ultimate problems and also in terms of demonstrating to donors that something is being done. However, unless and until the ultimate causal factors, such as ethics, human behavior and population growth are dealt with, long-term and effective conservation will remain problematic. In spite of

Table I. A general framework for analyzing and solving conservation problems

| Problem | Class of problem | Solution | Time frame |
|---|--------------------|----------------------------------|----------------|
| Violations of law Legislation | Proximate | Law enforcement | Short |
| | Proximate | Lobbying & financial incentives | Medium to long |
| Values/ethics | Proximate/ultimate | Education | Long |
| Population growth/ hyper-consumption | Ultimate | Education & financial incentives | Long |
| Management of parks & other nat. resources | Proximate/ultimate | Research/monitoring | Medium to long |

this, it must be emphasized that some proximate factors, such as violation of the law, will require attention in perpetuity because of human nature. No society anywhere or at any time has ever been free of the need for laws and law enforcement.

I also stress that for any given PA the relative importance of the various problems and possible solutions will change over time because of landscape dynamics and their corresponding impacts on the PA and because of intrinsic biotic and abiotic changes within the PA.

Concluding Recommendations

In terms of conserving tropical forest protected areas (PAs), several researchers (Brandon, 1997, 2002; Brockelman *et al.*, 2002; MacKinnon, 1997; Oates, 2002; Struhsaker, 1997, 1999, 2001 and web site: <http://www.frameweb.org/> [select Thematic Topics, Ecosystems, Forests and then documents under Africa's Rain Forest Protected Areas: Problem and Possible Solutions]; Struhsaker *et al.*, 2005; Terborgh, 2002; Terborgh and van Schaik, 1997; Tutin, 2002; van Schaik and Kramer, 1997; van Schaik *et al.*, 2002) have made the case for giving highest priority to the following issues:

- 1) improve law enforcement with greater technical and financial support;
- 2) extend boundaries of current PAs wherever possible and create more, large PAs;
- 3) develop secure and long-term funding for PA support;
- 4) develop strategies that are effective in winning the support of neighboring communities for the PA;
- 5) develop strategies that deal with 3 ultimate causal factors:
 - a) attitudes and value systems sympathetic to conservation;
 - b) stabilizing human population size; and
 - c) stabilizing or reducing levels of consumption of natural resources;
- 6) establish biological monitoring programs in forest PAs to evaluate the success of conservation management practices and to anticipate future conservation problems, such as those related to intrinsic, biological dynamics within the PA; and
- 7) curtail corruption.

Implementation of these recommendations is fundamental to the conservation not only of red colobus monkeys and their habitats, but for the conservation of most tropical forest species as well.

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REFERENCES

- Brockelman, W. Y., Griffiths, M., Rao, M., Ruf, R., and Salafsky, N. (2002). Enforcement mechanisms. In Terborgh, J., van Schaik, C., Davenport, L., and Rao, M. (eds.), *Making Parks Work: Strategies for Preserving Tropical Nature*, Island Press, Washington, Covelo, and London, pp. 265–278.
- Brandon, K. (1997). Policy and practical considerations in land-use strategies for biodiversity conservation. In Kramer, R., van Schaik, C., and Johnson, J. (eds.), *Last Stand: Protected Areas and the Defense of Tropical Biodiversity*, Oxford University Press, New York and Oxford, pp. 90–114.
- Brandon, K. (2002). Putting the right parks in the right places. In Terborgh, J., van Schaik, C., Davenport, L., and Rao, M. (eds.), *Making Parks Work: Strategies for Preserving Tropical Nature*, Island Press, Washington, Covelo, and London, pp. 443–467.
- Butynski, T. M., and Koster, S. H. (1994). Distribution and conservation status of primates in Bioko Island, Equatorial Guinea. *Biodivers. Conserv.* 3: 893–909.
- Butynski, T. M., and Mwangi, G. (1995). Census of Kenya's endangered red colobus and crested mangabey. *Afr. Primates* 1: 8–10.
- Camperio Ciani, A., Palentini, L., and Finotto, E. (2001). Survival of a small translocated *Procolobus kirkii* population on Pemba Island. *Anim. Biodivers. Conserv.* 24: 15–18.
- Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J. P., and Struhsaker, T. T. (2000). Long-term effects of logging on African primate communities: A 28-year comparison from Kibale National Park, Uganda. *Conserv. Biol.* 14: 207–217.
- Chapman, C. A., Chapman, L. J., Bjorndal, K. A., and Onderdonk, D. A. (2002). Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. *Int. J. Primatol.* 23: 283–310.
- Chapman, C. A., and Lambert, J. E. (2000). Habitat alteration and the conservation of African primates: Case study of Kibale National Park, Uganda. *Am. J. Primatol.* 50: 169–185.
- Colyn, M. (1991). L'importance zoogeographique du bassin du fleuve Zaïre pour spéciation: le cas des primates simiens. *Musee Royal de l'Afrique Centrale Annales Sciences Zoologiques*. vol. 264. 250 pp.
- Davies, A. G. (1987). *The Gola Forest Reserves, Sierra Leone: Wildlife Conservation and Forest Management*. IUCN, Gland, Switzerland and Cambridge.
- Dinesen, L., Lehberg, T., Rahner, M. C., and Fjeldsa, J. (2001). Conservation priorities for the forests of the Udzungwa Mountains, Tanzania, based on primates, duikers and birds. *Biol. Conserv.* 99: 223–236.
- Dowsett-Lemaire, F., and Dowsett, R. J. (2001). A new population of gorillas *Gorilla gorilla* and other endangered primates in western Cameroon. *Afr. Primates* 5: 3–7.
- Edwards, A. E. (1992). *The Diurnal Primates of Korup National Park, Cameroon: Abundance, Productivity and Polyspecific Associations*. Unpublished MSc., University of Florida, Gainesville, 116 pp.
- Ehardt, C. L., Struhsaker, T. T., and Butynski, T. M. (1999). *Conservation of the Endangered Endemic Primates of the Udzungwa Mountains, Tanzania: Surveys, Habitat Assessment, and Long-term Monitoring*. Unpublished report to The Margot Marsh Biodiversity Fund and the World Wide Fund for Nature—Tanzania, 103 pp.
- Gautier-Hion, A., Colyn, M. and Gautier, J.-P. (1999). *Histoire Naturelle des Primates D'Afrique Centrale*. ECOFAC, Libreville, 162 pp.
- Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C. P., and Struhsaker, T. T. (2003). An assessment of the diversity of African Primates. *Int. J. Primatol.* 24: 1301–1357.

- Grubb, P., and Powell, C. B. (1999). Discovery of red colobus monkeys (*Procolobus badius*) in the Niger Delta with the description of a new and geographically isolated subspecies. *J. Zool. Lond.* 248: 67–73.
- Grubb, P., Struhsaker, T. T., and Siex, K. S. (in press.) In Kingdon, J., Happold, D., and Butynski, T. M. (eds.), *Mammals of Africa*, Academic Press, London.
- Hughes, F. M. R. (1985). *The Tana River Floodplain Forest, Kenya: Ecology and the Impact of Development*. Unpublished Ph.D. Thesis, University of Cambridge, Cambridge, 421 pp.
- Infield, M. (1988). *Hunting, trapping and fishing in villages within and on the periphery of the Korup National Park*. Unpublished Paper No. 6 of the Korup National Park Socio-Economic Survey. Publication 3206/a9.6. World Wildlife Fund, Gland, Switzerland.
- Johns, A. D., and Skorupa, J. P. (1987). Responses of rainforest primates to habitat disturbance: A review. *Int. J. Primatol.* 8: 157–191.
- Kingdon, J. (1974). *East African Mammals*. Vol. 1, Academic Press, London and New York, 446 pp.
- Kingdon, J. (2001). *The Kingdon Field Guide to African Mammals*, Academic Press, London and San Diego, 476 pp.
- Martin, C., and Asibey, E. O. A. (1979). Effect of timber exploitation on primate population and distribution in the Bia rain forest area of Ghana. Unpublished paper delivered at the 7th Congress of the International Primatological Society, Bangalore, India.
- MacKinnon, K. (1997). The ecological foundations of biodiversity protection. In Kramer, R., van Schaik, C., and Johnson, J. (eds.), *Last Stand: Protected Areas and the Defense of Tropical Biodiversity*. Oxford University Press, New York and Oxford, pp. 36–63
- Mbora, D. N. M. (2003). *Habitat Quality and Fragmentation and the Distribution and Abundance of the Tana River Red Colobus Monkey, Procolobus rufomitratu, in Eastern Kenya*. Unpublished Ph.D. Thesis, Miami University, 145 pp.
- McGraw, W. S., and Oates, J. F. (2002). Evidence for a surviving population of Miss Waldron's red colobus. *Oryx* 36(3): 223.
- Mitani, J. C., Struhsaker, T. T., and Lwanga, J. S. (2000). Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: Implications for conservation and census methods. *Int. J. Primatol.* 21: 269–286.
- Oates, J. F. (1986–1990). *Action Plan for African Primate Conservation: 1986–1990*. IUCN/SSC Primate Specialist Group, 41 pp.
- Oates, J. F. (1996). *African Primates: Status Survey and Conservation Action Plan Revised Edition*. IUCN/SSC Primate Specialist Group, 80 pp.
- Oates, J. F. (1999). *Myth and Reality in the Rain Forest: How Conservation Strategies are Failing in West Africa*, University of California Press, Berkeley, Los Angeles, London. 310 pp.
- Oates, J. F. (2002). West Africa: Tropical forest parks on the brink. In Terborgh, J., van Schaik, C., Davenport, L., and Rao, M. (eds.), *Making Parks Work: Strategies for Preserving Tropical Nature*, Island Press, Washington, Covelo, and London, pp. 57–75.
- Oates, J. F., Abedi-Lartey, M., McGraw, W. S., Struhsaker, T. T., and Whitesides, G. H. (2000). Extinction of a west African red colobus monkey. *Conserv. Biol.* 14: 1526–1532.
- Pope, T. R. (1995). Socioecology, population fragmentation, and patterns of genetic loss in endangered primates. In Avis, J., and Hamrick, J. (eds.), *Conservation Genetics: Case histories from nature*. Chapman and Hall, New York, pp. 119–159.
- Rahm, U. H. (1970). Ecology, zoogeography, and systematics of some African forest monkeys. In Napier, J. R., and Napier, P. H. (eds.), *Old World Monkeys*, Academic Press, New York and London. pp. 589–626.
- Robinson, J. G., and Bennett, E. L. (eds.) (2000). *Hunting for Sustainability in Tropical Forests*, Columbia University Press, New York, 582 pp.
- Rodgers, W. A., and Homewood, K. M. (1982). Biological values and conservation prospects for the forests and primate populations of the Uzungwa Mountains, Tanzania. *Biol. Conserv.* 24: 285–304.
- Siex, K. S. (2003). *Effects of population compression on the demography, ecology, and behavior of the Zanzibar red colobus monkey (Procolobus kirkii)*. Unpublished Ph.D. Thesis, Duke University, 314 pp.

- Skorupa, J. P. (1986). Responses of rainforest primates to selective logging in Kibale Forest, Uganda: A summary report. In Benirschke, K. (ed.), *Primates: The Road to Self-Sustaining Populations*. Springer-Verlag, New York, pp. 57–70.
- Skorupa, J. P. (1988). *The Effects of Selective Timber Harvesting on Rain-Forest Primates in Kibale Forest, Uganda*. Unpublished Ph.D. Thesis, University of California, Davis, 519 pp.
- Stanford, C. B. (1998). *Chimpanzee and Red Colobus: The Ecology of Predator and Prey*, Harvard University Press, Cambridge, 296 pp.
- Struhsaker, T. T. (1975). *The Red Colobus Monkey*, University of Chicago Press, Chicago, 311 pp.
- Struhsaker, T. T. (1997). *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. University Press of Florida, Gainesville, FL. 434 pp.
- Struhsaker, T. T. (1999). Primate communities in Africa: The consequence of long-term evolution or the artifact of recent hunting? In Fleagle, J. G., Janson, C., and Reed, K. E. (eds.), *Primate Communities*, Cambridge University Press, Cambridge, UK, pp. 289–294.
- Struhsaker, T. T. (2000). Variation in adult sex ratios of red colobus monkey social groups: Implications for interspecific comparisons. In Kappeler, P. M. (ed.), *Primate Males*, Cambridge University Press, Cambridge, UK, pp. 108–119.
- Struhsaker, T. T. (2001). *Africa's Rain Forest Protected Areas: Problems and Possible Solutions*. An Unpublished Report to the Center for Applied Biodiversity Science, Conservation International, Washington, DC, 55 pp.
- Struhsaker, T. T. (2002). Strategies for conserving forest national parks in Africa with a case study from Uganda. In Terborgh, J., van Schaik, C., Davenport, L., and Rao, M. (eds.), *Making Parks Work: Strategies for Preserving Tropical Nature*. Island Press, Washington, DC, pp. 97–111.
- Struhsaker, T. T., Marshall, A. R., Detwiler, K., Siex, K. S., Ehardt, C., Dahl-Lisbjerg, D., and Butynski, T. M. (2004). Demographic variation in the Udzungwa red colobus (*Procolobus gordonorum*) in relation to gross ecological and sociological parameters. *Int. J. Primatol.* 25: 615–658.
- Struhsaker, T. T., and Leland, L. (1979). Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. In Rosenblatt, J. S., Hinde, R. A., Beer, C. and Busnel, M. C. (eds.) *Advances in the Study of Behavior*. Vol. 9, Academic Press, New York, pp. 159–228.
- Struhsaker, T. T., and Pope, T. R. (1991). Mating system and reproductive success: A comparison of two African forest monkeys (*Colobus badius* and *Cercopithecus ascanius*). *Behavior* 117: 182–205.
- Struhsaker, T. T., and Siex, K. S. (1998). The Zanzibar red colobus monkey: Conservation status of an endangered island endemic. *Primate Conserv.* 18: 51–58.
- Struhsaker, T. T., Struhsaker, P. J., and Siex, K. S. (2005). Conserving Africa's Rain Forests: Problems and Possible Solutions. *Bio. Conserv.* 123: 45–54.
- Terborgh, J. (2002). Overcoming impediments to conservation. In Terborgh, J., van Schaik, C., Davenport, L., and Rao, M. (eds.), *Making Parks Work: Strategies for Preserving Tropical Nature*, Island Press, Washington, Covelo, and London. pp. 243–249.
- Terborgh, J., and van Schaik, C. P. (1997). Minimizing species loss: The imperative of protection. In Kramer, R., van Schaik, C., and Johnson, J. (eds.), *Last Stand: Protected Areas and the Defense of Tropical Biodiversity*, Oxford University Press, New York and Oxford, pp. 15–35.
- Thompson, J. A. M. (1999–2000). Conservation of Thollon's red colobus *Piliocolobus tholloni*, Democratic Republic of Congo. *Afr. Primates* 4: 27–32.
- Tutin, C. E. G. (2002). Parks in the Congo basin: Can conservation and development be reconciled? In Terborgh, J., van Schaik, C., Davenport, L., and Rao, M. (eds.), *Making Parks Work: Strategies for Preserving Tropical Nature*, Island Press, Washington, Covelo, and London, pp. 76–85.
- van Schaik, C. P., and Kramer, R. A. (1997). Toward a protection paradigm. In Kramer, R., van Schaik, C., and Johnson, J. (eds.), *Last Stand: Protected Areas and the Defense of Tropical Biodiversity*, Oxford University Press, New York and Oxford, pp. 212–230.

- van Schaik, C., Teborgh, J., Davenport, L., and Rao, M. (2002). In Terborgh, J., van Schaik, C., Davenport, L., and Rao, M. (eds.), *Making Parks Work: Strategies for Preserving Tropical Nature*, Island Press, Washington, Covelo, and London, pp. 468–481.
- Waltert, M., Lien, Faber, K., and Muhlenberg, M. (2002). Further declines of threatened primates in the Korup Project Area, south-west Cameroon. *Oryx* 36: 257–265.
- Watts, D. P., and Mitani, J. C. (2002). Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.* 23: 1–28.
- Werre, J. L. R. (2000). *Ecology and Behavior of the Niger Delta Red Colobus Monkey (Procolobus badius epieni)*. Unpublished Ph.D. Thesis, City University of New York, 222 pp.
- Wieczkowski, J., and Mbora, D. N. M. (1999–2000). Increasing threats to the conservation of endemic endangered primates and forests of the lower Tana River, Kenya. *Afr. Primates* 4: 32–40.
- World Resources Institute (2000). *World Resources 2000–2001*, Elsevier Science, Amsterdam, 389 pp.
- Wrangham, R. W., and Bergmann-Riss, E. L. (1990). Rates of predation on mammals by Gombe chimpanzees, 1972–1975. *Primates* 38: 157–170.