

# The value of unprotected habitat in conserving the critically endangered Tana River red colobus (*Procolobus rufomitratu*s)

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## Abstract

We determined the importance of unprotected forest habitat outside the Tana River Primate National Reserve (TRPNR), Kenya, in conserving the critically endangered Tana red colobus. We compared colobus and forest attributes inside and outside the reserve and found no significant difference in colobus density or mean group size, although absolute values for both measures were higher outside the reserve. Forests outside TRPNR had a higher basal area of trees, basal area per tree, and basal area of stumps from human use. We also compared data on group size and composition collected inside and outside TRPNR during the period of reserve establishment (1978), 10 years after establishment (1988) and over 20 years after establishment (2000). Mean group size declined by nearly 50% since the reserve was established across all age classes both inside and outside TRPNR. Since the red colobus population is in decline and forests outside TRPNR are as suitable as those inside as colobus habitat, we recommend adopting a community-based conservation strategy of sustainable forest management and use outside TRPNR to enhance conservation goals. © 2004 Elsevier Ltd. All rights reserved.

**Keywords:** Endemic; Flagship species; Kenya; Parks; Primates; Reserves

## 1. Introduction

Parks and reserves are typically considered the most effective means of protecting biodiversity (IUCN, 1984). However, parks and reserves are vulnerable to a wide array of anthropogenic threats (Bruner et al., 2001; Schaller, 1994; van Schaik and Kramer, 1997) and there is a widespread perception that they do not effectively conserve biodiversity. This perception has led to efforts to promote conservation of habitats found outside protected areas (Western et al., 1994). Nevertheless, only a few studies have tested whether differences in habitat conditions inside and outside parks and reserves influence their success at maintaining biodiversity. Liu et al.

(2001) reported that after the creation of the Wolong Nature Reserve to protect the giant panda (*Ailuropoda melanoleuca*) in China, rates of habitat degradation became higher inside than outside the reserve. In contrast, a questionnaire-based study by Bruner et al. (2001) found that most managers of tropical parks believe that habitat clearance, grazing, hunting and fire damage are less of a problem within than outside boundaries of parks and reserves (Bruner et al., 2001). Thus, there is a need for studies that actually measure habitat conditions inside and outside parks and reserves in order to determine the relative importance of unprotected habitat for conserving endangered and threatened species.

One ecosystem that is threatened by human impact and has several endemic and threatened species is the Tana River ecosystem in eastern Kenya. It is found in the lower floodplain of the Tana River comprising scattered forest patches of various sizes, on both sides of the river (Fig. 1). The forests are of great conservation importance because they support a high diversity of rare plant and animal species, and are part of the east African coastal

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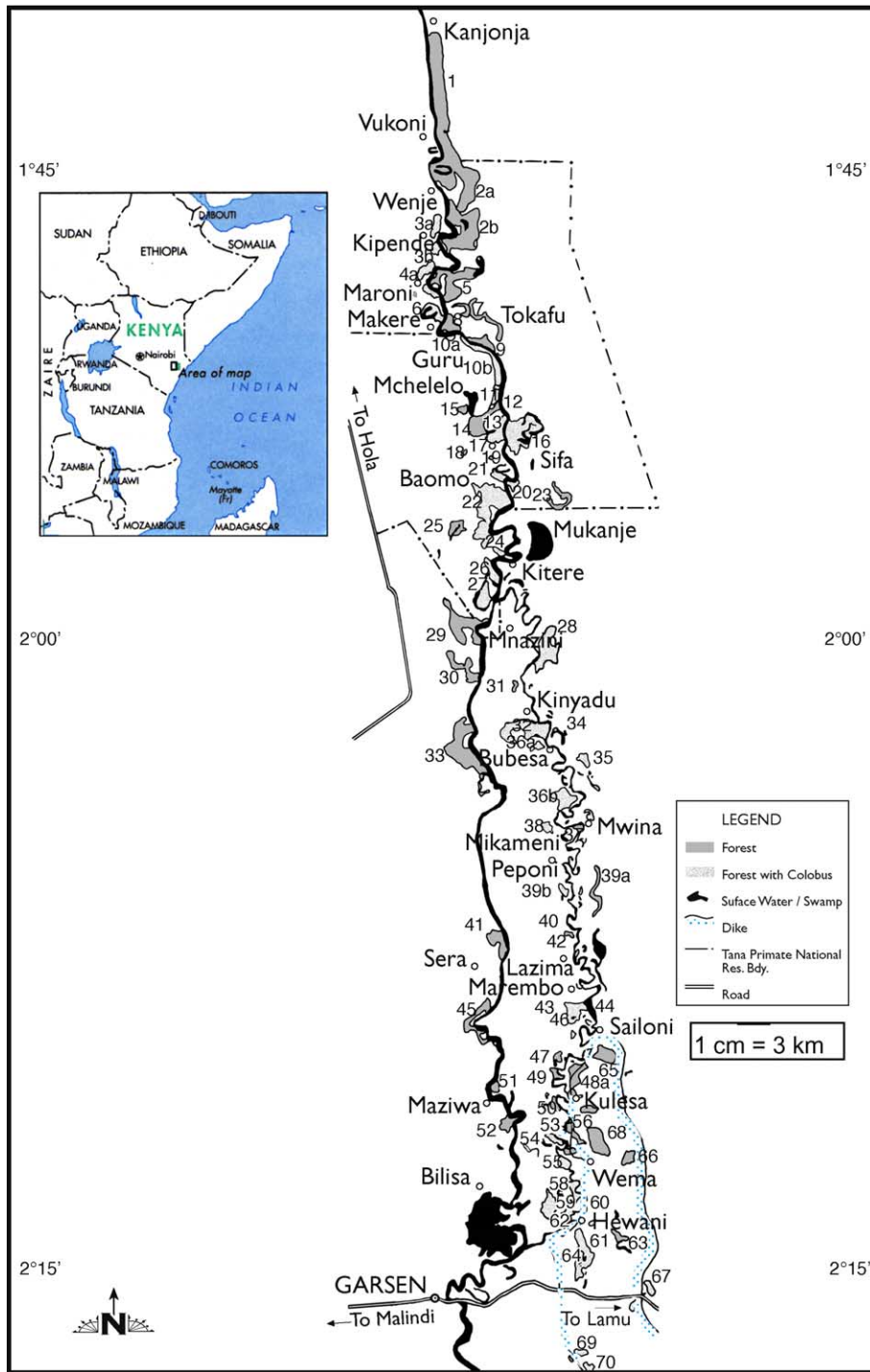


Fig. 1. Distribution of forest patches (numbered) along the Tana River and the location of the Tana River Primate National Reserve (TRPNR). This figure is adapted from Butynski and Mwangi (1994) and World Bank (1996).

forests global biodiversity hotspot (Andrews et al., 1975; Myers et al., 2000). In particular, they provide habitat for eight non-human primate species, including two endemic species, the Tana River red colobus (*Procolobus rufomitratu*s) and mangabey (*Cercocebus galeritu*s). The two are critically endangered and listed among the 25 most endangered primate taxa in the world (Grubb et al., 2003;

Mittermeier et al., 2002). In 1976, the Government of Kenya established Tana River Primate National Reserve (TRPNR) to protect representative forest communities and conserve the endemic primates (Marsh, 1976). However, a comprehensive census conducted in 1994 revealed that the populations of the two species were declining 20 years after TRPNR was established, and

that only 37% of colobus groups and 56% of mangabey groups were resident within TRPNR (Butynski and Mwangi, 1994). Forest habitat found outside TRPNR is likely vital for the long-term population viability of these critically endangered species. Consequently, there is a need for a quantitative analysis to determine the relative importance of habitat inside and outside TRPNR for the conservation of these primates.

Both the red colobus and the crested mangabey are flagship species for the conservation of this area (Seal et al., 1991). We chose to use the red colobus population for this analysis for several reasons. Colobus have a wider distribution in the habitat than the mangabeys; in 1994 red colobus were found in 50% of the forests but mangabeys in only 40% (Butynski and Mwangi, 1994). Also, colobus are easier to census than mangabeys because they have high site fidelity and are restricted to the canopy, thus reducing their vagility (Marsh, 1981). In contrast, mangabeys are terrestrial, vagile, very wary and therefore much more difficult to census (Homewood, 1976; Kinnaird, 1990; Wiczowski, 2003). Additionally, unlike colobus, mangabeys are not completely forest dependent due to their more varied diet composed of seeds, ripe fruit and animal matter that requires them to range widely over the landscape (Homewood, 1976; Kinnaird, 1990; Wiczowski, 2003).

If the TRPNR has been more successful at protecting habitat critical to red colobus than forests outside the reserve, we predicted that forests outside would show lower values for canopy tree density, basal area, and mean basal area per tree, but higher values for measures reflecting human use such as density and basal area of cut stems. In addition, we expected that the density of colobus monkeys outside the reserve would be lower, and mean group size would be smaller, reflecting the disturbance and degradation of forests outside through human use. In the analysis of change in group size and composition over time, we expected that if the TRPNR has been more successful at protecting habitat than forests outside the reserve, then colobus groups outside the reserve would show characteristics reflecting a decline in habitat quality. Specifically, the mean group size and the ratio of immature animals to adult females (a measure of replacement rates; Wilson and Bossert, 1971) outside the reserve would decline over time while they would remain stable or increase inside the reserve.

## 2. Methods

### 2.1. Study area

The floodplain of the Tana River in eastern Kenya supports approximately 26 km<sup>2</sup> of riparian forest patches (size range  $\approx$  1–500 ha) between latitudes 2°15' and 1°40'

South in an otherwise semi-arid thorn scrub environment (Fig. 1). The area has a flat topography that does not exceed 40 m above sea level, and a mean annual rainfall of only 400 mm. Thus, the area is semi-arid, and forests are created and maintained by groundwater and periodic flooding of the river. Hughes (1990) showed that availability of moisture from the river channel is the main environmental gradient influencing forest development, and that the lateral extent of forests depends on the depth of the water table. Thus, forest structure and composition vary with distance from the river channel (Hughes, 1990) rather than from upstream to downstream. Additionally, the main gradient in forest community composition is decreasing density and basal area of trees with increasing distance of forests from the main river channel (Mboru, 2003; Mboru and Meikle, in press).

Between 1999 and 2001, we measured colobus monkey density, mean group size and composition, as well as forest habitat attributes inside and outside the TRPNR. We then compared our data on group size and composition to those collected around the time of reserve establishment (Marsh, 1978) and 10 years after establishment (Decker, 1994). We hoped through these analyses to determine the relative importance of forests outside the reserve for the conservation of the Tana River red colobus, and by extension other species found in these forests.

### 2.2. Habitat analysis

We defined forest as a wooded area exceeding 1 ha and composed mainly of trees greater than 10 m in height and with a canopy cover exceeding 50%. We calculated forest area, perimeter, and area-to-perimeter ratios from a Geographic Information System of digitized aerial photographs taken in 1994 and 1996. To capture the range of habitat conditions within the entire floodplain, 15 forests inside and 16 forests outside TRPNR were studied. We chose forests so that approximately equal areas of forest were sampled inside and outside the TRPNR for both occupied and unoccupied forests. Eleven of the 31 forests were not occupied by colobus at the time of the study (five inside and six outside) but were included because they represented potential colobus habitat.

We followed the methodology described in Mboru and Meikle (in press). Within each forest, we systematically established evenly spaced vegetation belt transects running from a baseline on the riverbank side directly outwards to the edge of the forest patch (i.e. perpendicular to the river channel). Each belt was 5 m wide, and ran the width of the forest, with a maximum length of 100 m. The orientation of transects allowed for a detection of changes along the main environmental gradient in the system, the increasing depth of the water table away from the river channel in the floodplain

(Hughes, 1990). The number of transects sampled in each forest was based on the area of the forest. We sampled a minimum of three transects in all forests up to 5 ha. For forests bigger than 5 ha, we added one belt transect for every 10-fold increase in area since species generally increase with area logarithmically rather than linearly, making this a more efficient approach than sampling a fixed percentage of the forest patch area (Gotelli and Colwell, 2001).

In each transect, we collected data for trees that were both  $\geq 10$  m in height and had a diameter at breast height (DBH) of  $\geq 10$  cm. We recorded species identity, height, and DBH of each tree. We also measured amount of canopy cover every 20 m by photographing (using a 35-mm lens) the canopy and later analyzing the photographs digitally to determine percentage cover. Forest disturbance and use by humans was documented by recording the DBH of cut stems or damaged trees along the transect.

### 2.3. *Red colobus* attributes

Data on colobus attributes were collected by systematically surveying forests for primate groups (National Research Council, 1981; Mhora and Meikle, in press). We began with a thorough survey of each study forest to determine the number of resident groups. Once the survey was completed, all groups encountered were followed over a period of at least five days each to determine the group size, sex and age composition of members following the age and sex categories used by Marsh (1978) and Decker (1994). Tana River red colobus exhibit exceptional site fidelity, have small home ranges and generally scatter in a few trees when feeding or resting (Marsh, 1981). Thus, it was relatively easy to find groups on subsequent observation days, to maintain contact with them, and to determine group composition. We followed the above survey method because it has been the standard method of counting primates in the Tana forests (Marsh, 1978, 1986; Butynski and Mwangi, 1994; Decker, 1994) and facilitates comparisons between censuses.

### 2.4. *Data synthesis and analysis*

We summarized the transect data for each study forest and treated each forest as a unit for all subsequent analyses. We calculated absolute values for basal area ( $\text{m}^2/\text{ha}$ ), density (individual trees/ha), and basal area per tree (Barbour et al., 1999). We also calculated absolute values for basal area and density of stumps remaining after trees were cut or otherwise damaged as a measure of human use of the forests, and for tree species important as food sources for the Tana red colobus. We used 13-food tree species that constitute  $\geq 80\%$  of the colobus diet (Marsh, 1981; Decker, 1994). Colobus

population density and social group composition, as well as habitat attributes, were then summarized for each forest. Two-sample *t* tests (Sokal and Rolf, 1981) were used to determine whether there were differences in social group characteristics or habitat attributes between forests inside and outside the reserve. To evaluate changes in colobus group size and structure over time, we used data from this study and from two earlier studies that focused on detailed observations of group composition (Marsh, 1978; Decker, 1994). The study by Marsh (1978) was conducted about the time TRPNR was established (mid-1970s), Decker (1994) conducted a similar study in the late 1980s, 10 years after reserve establishment, and our study took place about 25 years after establishment.

A Poisson regression, weighted by number of counts made for each group, was used to analyze changes in social group size over the three periods; and a logistic regression was used to analyze changes in composition and structure of groups (Kleinbaum et al., 1998). The Poisson regression analysis is a regression technique for modeling-dependent variables that describe count data and is analogous to standard multiple regression analysis; hence, multiple regression assumptions apply for this analysis (Kleinbaum et al., 1998). In particular, we assumed that censuses for the different time periods were independent because the three studies did not focus on the same social groups. In each of the regression analyses, we used a factorial design with inside and outside the reserve as input variables and the three periods (1978, 1988, and 2000) as fixed factors. All analyses were done using SAS version 8.1 (SAS Institute, Cary, NC.).

## 3. Results

### 3.1. *Differences in colobus and habitat attributes inside and outside TRPNR*

We recorded 613 colobus monkeys in 50 social groups in the 20 forest patches that were occupied. There was no statistically significant difference in density of colobus monkeys, density of social groups, or mean group size inside and outside the reserve (Table 1). Nevertheless, absolute values of colobus population attributes were higher outside TRPNR (Table 1). In particular, density of colobus monkeys outside TRPNR was more than double that found inside. We sampled a total area of 49,850  $\text{m}^2$  in 109 belt transects in the 31 study forests, and recorded 70 tree species in 34 families. Forests outside the reserve tended to have larger total basal area of trees per hectare, basal area per tree, higher basal area per food tree, and basal area of cut stems (Table 2). Forests inside TRPNR also tended to have larger area to perimeter ratio (Table 2). No other differences were detected.

Table 1

Two sample *t* tests for colobus population attributes per forest, inside (IN) and outside (OUT) TRPNR

Attribute	IN ( <i>n</i> = 10)		OUT ( <i>n</i> = 10)		df	<i>t</i> value	<i>p</i>
	Mean	SEM	Mean	SEM			
Mean group size	8.45	(0.71)	11.34	(1.5)	10	−1.72	0.12
Colobus per hectare	0.54	(0.10)	1.34	(0.41)	7	−1.87	0.10
Number of groups	2.90	(0.77)	3.12	(0.95)	14	−0.18	0.86
Groups per hectare	0.07	(0.01)	0.10	(0.02)	11	−1.38	0.20

Table 2

Two sample *t* tests for forest habitat attributes<sup>a</sup> inside (IN) and outside (OUT) TRPNR

Attribute	IN ( <i>n</i> = 15)		OUT ( <i>n</i> = 16)		df	<i>t</i> value	<i>p</i> <sup>b</sup>
	Mean	SEM	Mean	SEM			
Absolute basal area of food trees (m <sup>2</sup> /ha)	22.20	(3.79)	43.06	(11.84)	18	1.68	0.11
Basal area per food tree (m <sup>2</sup> )	0.24	(0.04)	0.42	(0.09)	18	1.89	0.08
Absolute basal area of all trees (m <sup>2</sup> /ha)	42.60	(6.10)	71.11	(11.55)	23	2.18	0.04
Basal area per tree (m <sup>2</sup> )	0.13	(0.02)	0.20	(0.03)	22	2.12	0.05
Absolute basal area of stumps (m <sup>2</sup> /ha)	4.34	(1.18)	7.924	(1.47)	28	1.9	0.07
Absolute density of food trees (no./ha)	98.19	(14.13)	94.23	(15.57)	29	−0.19	0.85
Forest area-to-perimeter ratio	145.82	(15.79)	109.36	(9.99)	24	−1.95	0.06

<sup>a</sup> Comparisons shown are for those attributes important in determining colobus abundance (Mbora and Meikle, in press), and with *p* ≤ 0.1.<sup>b</sup> All *p* values are not significant after a Bonferroni adjustment (Sokal and Rolf, 1981).

### 3.2. Change in colobus group size and structure over time

We analyzed data from 13 groups (*n* = 11 inside and 2 outside TRPNR) studied by Marsh in 1978, and 15 groups (*n* = 6 inside and 9 outside) studied by Decker in 1988, and the 50 groups in 1999–2001 (*n* = 27 inside, 23 outside; Mbora and Meikle, in press). Although some of the earlier estimates were based on rather small sample sizes, we found significant differences in mean group size over the three periods. Additionally, this difference depended strongly on the location, inside or outside the reserve (Poisson regression;  $\chi^2 = 18.86$ , *df* = 2, *p* < 0.00, Fig. 2). In 1978, the mean group size was close to 20 animals both inside and outside TRPNR, but this declined significantly by 1988 in both areas ( $\chi^2 = 5.72$ , *df* = 1, *p* < 0.02). In 1988, the mean group size outside TRPNR was nine animals, which was significantly lower than the mean of 12 animals per group inside the reserve ( $\chi^2 = 5.96$ , *df* = 1, *p* < 0.02, Fig. 2). Mean group size declined further inside TRPNR between 1988 and 2000 ( $\chi^2 = 18.83$ , *df* = 1, *p* < 0.00, Fig. 2). But, during that period, the mean group size outside TRPNR increased to 11 animals, which was not significantly different from inside TRPNR, which stood at about 10 animals ( $\chi^2 = 1.11$ , *df* = 1, *p* < 0.29, Fig. 2).

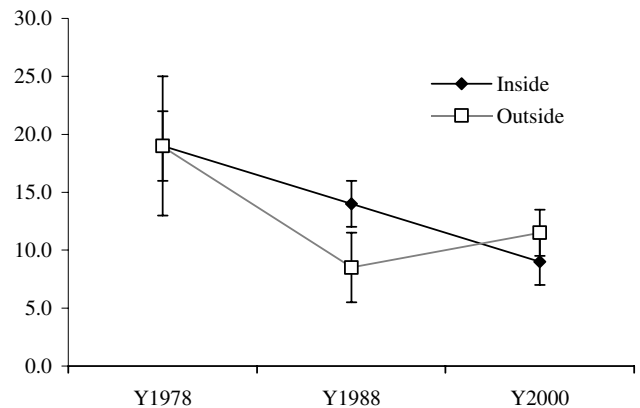


Fig. 2. Mean colobus group size, 1978, 1988, and 2000, inside and outside TRPNR (bars are 95% CI).

The mean proportion of immature animals in each group did not differ inside and outside or between the years over the 25-year period (Fig. 3). Consequently, the ratio of immature individuals (infants and juveniles) to adult females, a crude measure of population replacement rate (Wilson and Bossert, 1971; Zucker and Clarke, 2003), did not differ between inside and outside the reserve ( $\chi^2 = 1.10$ , *df* = 1, *p* = 0.29), between years ( $\chi^2 = 1.66$ , *df* = 2, *p* = 0.44) or show any significant

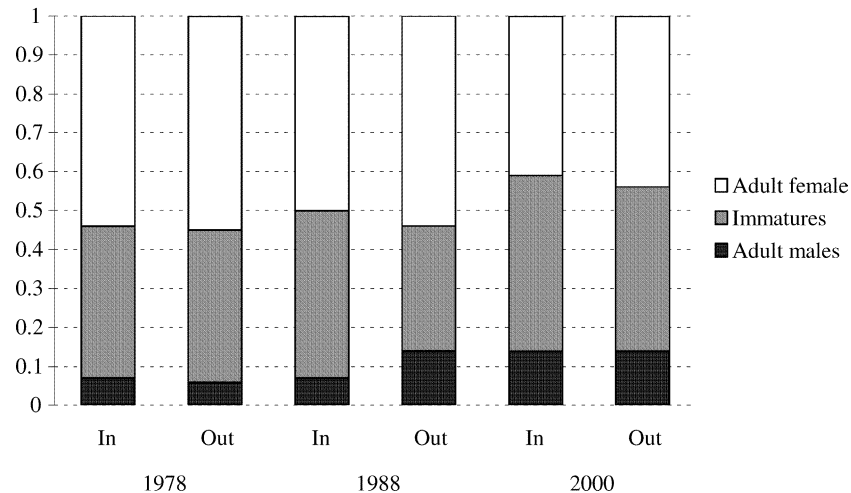


Fig. 3. Proportions of adult females, immature animals and adult males in a group, 1978, 1988, and 2000, inside and outside TRPNR.

interaction between the year and location ( $\chi^2 = 1.5$ ,  $df = 2$ ,  $p = 0.47$ ). However, the proportion of adult females among adults per group declined significantly between the years ( $\chi^2 = 8.87$ ,  $df = 2$ ,  $p < 0.01$ ; Fig. 3), although it did not differ inside and outside of the reserve ( $\chi^2 = 2.83$ ,  $df = 1$ ,  $p < 0.09$ ).

#### 4. Discussion

##### 4.1. Habitat and colobus attributes inside and outside TRPNR

We expected that TRPNR forests would have been protected by their reserve status and would therefore show higher values for habitat attributes such as canopy tree density, basal area ( $m^2/ha$ ) and mean basal area per tree, as well as lower values for measures reflecting human use, such as density and basal area of cut stems. In accordance with results recorded by Mhora and Meikle (in press), and studies of red colobus elsewhere (Chapman et al., 2000), we expected a higher density of colobus monkeys and possibly larger social groups inside the reserve than outside as a consequence of the degradation of forests outside through human use. Contrary to these predictions, we found no difference between forests inside and outside TRPNR with regard to colobus population attributes (Table 1). Interestingly, all colobus population attributes tended to be slightly higher outside, although the differences were not statistically significant. Nonetheless, the difference in density of colobus monkeys (absolute values) between the two locations was striking; density of colobus monkeys outside TRPNR was more than double that found inside. Similarly, we found that forests outside tended to have larger basal area of canopy trees and basal area per tree, even though it was not statistically significant. However, in accordance with our predictions, basal area of cut stems was higher in forests

outside TRPNR. Our results indicate that forests outside TRPNR provide habitat for colobus monkeys that is at least as good as the forests inside the reserve.

##### 4.2. Change in group size and structure over time

The analysis of group size changes over time shows a consistent and significant decline of nearly 50% in the colobus group size both inside and outside the reserve (Fig. 2) mostly affecting adult females (Fig. 3). Evidence from other primate populations suggests that when food resources decline, priority of access to food is limited to high-ranking animals in the population and mortality is highest among young and subordinate animals (Cheney et al., 1981; Struhsaker, 1976; Altmann et al., 1985). This may explain the tendency for an increase in the proportion of adult males among all adults (Fig. 3), and the declines in the proportion of adult females (Fig. 3) since the reserve was established. Although it is difficult to determine replacement rates directly for primates (Wilson and Bossert, 1971), the ratio of immature animals to adult females is usually considered a good, though crude, measure of replacement rates (Zucker and Clarke, 2003). It is interesting that despite the reduced group size and changes in adult ratios in the red colobus, the ratio of immatures remained unchanged over time both inside and outside TRPNR.

The decline seen in the colobus population is likely related to the habitat deterioration caused by increasing human use of forests and concomitant declines in food resources (Wieczkowski and Mhora, 1999–2000) because environmental change can be a major cause of primate population decline. For example, a complex suite of factors operating in the Amboseli basin, Kenya (Western and Van Praet, 1973) resulted in reduction of food resources and precipitous declines of populations of yellow baboons (*Papio cynocephalus*) and vervet monkeys (*Cercopithecus aethiops*). Between 1960 and

1969, the population of yellow baboons declined at a staggering rate of 38% per annum (Hausfater, 1975; Altmann et al., 1985), and the vervet monkey population declined at a rate of 6.8% per annum between 1963 and 1986 (Struhsaker, 1976; Lee and Hauser, 1998).

The pattern of population decline evident in the Tana River red colobus corresponds to habitat changes over the past four decades. During the 1960s, civil unrest near the Kenya–Somali border caused many people living on the east bank of Tana River to move to the west bank (Decker, 1994; Marsh, 1976). This caused increased forest clearing for cultivation, and loss of 17% of forest cover between 1960 and 1975 (Marsh, 1986) within the range of the colobus. This was the primary motivation to establish the TRPNR in 1976. It was hoped that establishment of TRPNR would lead to enhanced patrols to stop further cutting of forest, and that families resident within would be compensated for permanent crops and relocated to land outside TRPNR (Marsh, 1976). However, since the TRPNR did not raise any revenues from tourism, it was probably considered a low priority reserve by the government and received little subsidy for management activities (Marsh, 1976). Thus, in the 1970s and early 1980s TRPNR remained largely a “paper park” with virtually no management.

In the mid-1980s, the populations of the two endemic primates had declined precipitously since the establishment of TRPNR (Marsh, 1986). This led to renewed concern and the Kenya Wildlife Service posted a warden to the reserve and conducted a Population and Habitat Viability Assessment (PHVA; Seal et al., 1991). The PHVA concluded that the only long-term solution to the threats facing the ecosystem was the removal of all humans from the reserve. However, many local people vehemently opposed the idea of relocating from the reserve (World Bank, 1996).

In pursuance of the recommendations of the PHVA, but taking into account the sentiments of the local people, a Global Environment Facility (GEF) project was initiated in the early 1990s (World Bank, 1996). The project had three components, research and monitoring, reserve management, and community conservation and development. According to the project document (World Bank, 1996, p. 4) the core element of the community component was to “gain local support and co-operation for conservation by maintaining a positive dialogue”. By so doing, it was hoped that the people would eventually agree to a voluntary resettlement. However, this expected eventual outcome did not materialize. In contrast, our research shows that within the life of the GEF project, forest clearance and selective felling of large trees increased dramatically (Wieczkowski and Mhora, 1999–2000). Furthermore, we found strong anecdotal evidence that the forest clearance and selective felling of large trees we documented was malicious. In most villages we worked in, we repeatedly

heard the sentiment that the community felt that if there were no forests and monkeys, there would be no need to relocate them (Mhora, 2000a,b). Thus, we conjecture that the difference in pattern of decline between groups inside and outside between 1978 and 1988 (Fig. 2) was due to the fact that the reserve was established in the best remaining forested areas, evidenced by the highest density of groups (Marsh, 1976). However, forest cutting and degradation continued inside after 1988, apparently in opposition to the start of the GEF project, and caused forest habitat inside and outside to be more similar, but with forests outside having somewhat larger groups.

#### 4.3. Conservation implications

Since the establishment of TRPNR, the singular focus of conservation activities in the Tana has been on forests inside the reserve (World Bank, 1996; Seal et al., 1991). Yet our results indicate that these efforts have largely been ineffective and that forests outside TRPNR are probably as suitable as those inside as colobus habitat. Furthermore, a census done in 1994 showed that only 37% of colobus groups lived within TRPNR (Butynski and Mwangi, 1994). These findings call into question the conservation strategy pursued in the Tana, especially its emphasis on removal of humans from the reserve. Clearly, forest habitat outside TRPNR is vital for the conservation of this critically endangered primate, but it is also crucial that the effectiveness of TRPNR is enhanced.

Bruner et al. (2001) found that areas adjacent to, but not within the boundaries of reserves showed continued habitat clearing and degradation. They found that the main factors contributing to effectiveness of parks and reserves were the level of security presence and law enforcement (Bruner et al., 2001). Also important to the effectiveness, was the degree of border demarcation and number of direct compensation programs for people living in the surrounding areas. Thus, Bruner et al. (2001) suggested that modest increases in funding would greatly enhance the protective function of reserves. Our findings for TRPNR do not fit this general pattern of reserve effectiveness reported by Bruner et al. (2001). The reduction in the colobus population within TRPNR suggests that despite the presence of a warden and other park staff, law enforcement was insufficient (Mhora, 2000a,b; Wieczkowski and Mhora, 1999–2000) and that mere presence of law enforcement personnel was not a deterrent. Furthermore, TRPNR has been a recipient of large amounts of conservation funding (World Bank, 1996). However, the lack of an effective direct compensation program (Bruner et al., 2001) may have exacerbated destruction of forests within the reserve.

Since many local people have already expressed their displeasure with the establishment of TRPNR (Mhora,

2000a,b), designating forests outside as reserve area might increase their resentment. Hence, this is a situation where adopting a community-based conservation approach aimed at sustainable forest management and use may be appropriate (Western et al., 1994). Because forests outside TRPNR are not legally protected, the main conservation concern is that their owners could convert the land to other uses. Thus, a community-based conservation approach would entail providing incentives to maintain the status quo. Consequently, at least two possibilities can be pursued. One possibility is establishment of nature-based businesses such as ecotourism and butterfly farming (Gordon and Ayiemba, 2003). Another possibility is direct payments and easements for conservation of forests (Ferraro and Kiss, 2002). Under such a scheme, communities and landowners would be paid directly for the right to manage the site for conservation purposes under leasehold or alternative appropriate arrangements (Ferraro and Kiss, 2002).

Our study also indicates that flagship species (Caro and O'Doherty, 1999; Simberloff, 1998) can be important model species for demonstrating the value of unprotected habitats in protecting biodiversity. Flagship species are often used as a public relations tool to galvanize public support for biodiversity conservation (Western, 1987) and can be especially useful in indicating the value of unprotected habitats and in galvanizing conservation action (Caro and O'Doherty, 1999). Thus, we recommend that the findings of this study serve as a basis for comparison in determining the value of unprotected habitat for populations of flagship species in other parts of the world.

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### References

Altmann, J., Hausfater, G., Altmann, S.A., 1985. Demography of Amboseli baboons. *American Journal of Primatology* 8, 113–125.

- Andrews, P., Groves, C.P., Horne, J.F.M., 1975. Ecology of the lower Tana River floodplain (Kenya). *Journal of East African Natural History Society and National Museums* 151, 1–31.
- Barbour, M.G., Burk, J.H., Pitts, W.D., Gilliam, F.S., Schwartz, M.W., 1999. *Terrestrial Plant Ecology*, third ed. Benjamin/Cummings, Menlo Park, CA.
- Bruner, A.G., Gullison, R.E., Rice, R.E., da Fonseca, G.A.B., 2001. Effectiveness of parks in protecting tropical biodiversity. *Science* 291, 125–128.
- Butynski, T.M., Mwangi, G., 1994. Conservation status and distribution of the Tana River red colobus and crested mangabey. Report for: Zoo Atlanta, Kenya Wildlife Service, National Museums of Kenya, Institute of Primate Research, and East African Wildlife Society.
- Caro, T.M., O'Doherty, G., 1999. On the use of surrogate species in conservation biology. *Conservation Biology* 13, 805–814.
- Chapman, C.A., Balcomb, S.R., Gillespie, T.R., Skorupa, J.P., Struhsaker, T.T., 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conservation Biology* 14, 207–217.
- Cheney, D.L., Lee, P.C., Seyfarth, R.M., 1981. Behavioural correlates of non-random mortality among free ranging female vervet monkeys. *Behavioural Ecology and Sociobiology* 9, 153–161.
- Decker, B.S., 1994. Effects of habitat disturbance on the behavioural ecology and demographics of the Tana River red colobus (*Colobus badius rufomitratu*). *International Journal of Primatology* 15, 703–737.
- Ferraro, P.J., Kiss, A., 2002. Direct payments to conserve biodiversity. *Science* 298, 1718–1719.
- Gordon, I., Ayiemba, W., 2003. Harnessing butterfly biodiversity for improving livelihoods and forest conservation: the Kipepeo Project. *The Journal of Environment and Development* 12, 82–98.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4, 379–391.
- Grubb, P., Butynski, T.M., Oates, J.F., Bearder, S.K., Disotell, T.R., Groves, C.P., Struhsaker, T.T., 2003. Assessment of the diversity of African primates. *International Journal of Primatology* 24, 1301–1357.
- Hausfater, G., 1975. *Dominance and Reproduction in Baboons (Papio cynocephalus)*. Karger, Basel.
- Homewood, K.M., 1976. *The ecology and behaviour of the Tana mangabey*. Ph.D. Dissertation, University College, London.
- Hughes, F.M.R., 1990. The influence of flooding regimes on forest distribution and composition in the Tana River floodplain, Kenya. *Journal of Applied Ecology* 27, 475–491.
- International Union for Conservation Of Nature and Natural Resources, 1984. *Categories, Objectives and Criteria for Protected Areas*. In: McNeely, J.A., Miller, K.R. (Eds.), *National Parks Conservation and Development*. Smithsonian Institution Press, Washington DC, pp. 47–53.
- Kinnaird, M.F., 1990. Behavioural and demographic responses to habitat change by the Tana River Crested Mangabey (*Cercocebus galeritus galeritus*). Ph.D. Dissertation, University of Florida.
- Kleinbaum, D.G., Kupper, L.L., Muller, K.E., Nizam, A., 1998. *Applied Regression Analysis and Other Multivariable Methods*. Brooks/Cole Publishing Company, Pacific Grove, CA.
- Lee, P.C., Hauser, M.D., 1998. Long-term consequences of changes in territory quality on feeding and reproductive strategies of vervet monkeys. *Journal of Animal Ecology* 67, 347–358.
- Liu, J., Linderman, M., Ouyang, Z., An, L., Yang, J., Zhang, H., 2001. Ecological degradation: the case of Wolong nature reserve for giant pandas. *Science* 292, 98–101.
- Marsh, C.W., 1976. *A Management Plan for the Tana River Game Reserve*. A report to the Kenya Wildlife Conservation and Management Department, and the New York Zoological Society, New York.



- Marsh, C.W., 1978. Ecology and Social Organization of the Tana River Red Colobus (*Colobus badius rufomitratu*s). Ph.D. Dissertation, University of Bristol.
- Marsh, C.W., 1981. Diet choice among red colobus (*Colobus badius rufomitratu*s) on the Tana River, Kenya. *Folia Primatologica* 35, 147–178.
- Marsh, C.W., 1986. A re-survey of the Tana River primates and their habitat. *Primate Conservation* 7, 72–81.
- Mbora, D.N.M., 2000a. Assault on the lower Tana. *Swara* 23, 19–21.
- Mbora, D.N.M., 2000b. Saving the Tana. *Ecoforum* 24, 33–35.
- Mbora, D.N.M., 2003. Habitat quality and fragmentation and the distribution and abundance of the Tana River red colobus (*Procolobus rufomitratu*s) in eastern Kenya. Ph.D. Dissertation, Miami University.
- Mbora, D.N.M., Meikle, D.B., in press. Forest fragmentation and the distribution, abundance and conservation of the Tana River red colobus (*Procolobus rufomitratu*s). *Biological Conservation* 118(1), 67–77.
- Mittermeier, R.A., Konstant, W.R., Rylands, A.B., Ganzhorn, J., Oates, J.F., Butynski, T.M., Nadler, T., Supriatna, J., Padua, C.V., Rambaldi, D., 2002. Primates in peril: the world's top 25 most endangered primates-2002. Conservation International, Margot Marsh Biodiversity Foundation, IUCN/SSC, International Primatological Society.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- National Research Council, 1981. Techniques for the Study of Primate Population Ecology. National Academy of Sciences Press, Washington, DC.
- Schaller, G.B., 1994. The Last Panda. University of Chicago Press, Chicago.
- Seal, U.S., Lacy, R.C., Medley, K.E., Seal, R., Foose, T.J., 1991. Tana River primate reserve conservation workshop report. Captive Breeding Specialist Group (CBSG/SSC/IUCN).
- Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single species management passé in the landscape era? *Biological Conservation* 83, 247–257.
- Sokal, R., Rolf, F., 1981. Biometry. W.H. Freeman, San Francisco, CA.
- Struhsaker, T.T., 1976. A further decline in numbers of Amboseli vervet monkeys. *Biotropica* 8, 211–214.
- van Schaik, C.P., Kramer, R.A., 1997. Toward a protection paradigm. In: Kramer, R., van Schaik, C., Johnson, J. (Eds.), Last Stand: Protected Areas and The Defense of Biodiversity. Oxford University Press, New York, pp. 212–230.
- Western, D., 1987. Africa's elephants and rhinos: flagships in crisis. *Trends in Ecology* 2, 343–346.
- Western, D., Van Praet, C., 1973. Cyclical changes in the habitat and climate of an East African ecosystem. *Nature (London)* 241, 104–106.
- Western, D., Wright, R.M., Strum, S.C., 1994. Natural Connections: Perspectives in Community-Based Conservation. Island Press, Washington, DC.
- Wieczkowski, J.A., 2003. Aspects of the ecological flexibility of the Tana mangabey (*Cercocebus galeritus*) in its fragmented habitat, Tana River, Kenya. Ph.D. Dissertation, University of Georgia, Athens, GA.
- Wieczkowski, J., Mbora, D.N.M., 1999–2000. Increasing threats to the conservation of endemic endangered primates and forests of the lower Tana River, Kenya. *African Primates* 4, 32–40.
- Wilson, E.O., Bossert, W.H., 1971. A Primer of Population Biology. Sinauer Associates, Sunderland, MA.
- World Bank, 1996. The republic of Kenya: Tana River primate national reserve. Project document. The World Bank, Washington, DC.
- Zucker, E.L., Clarke, M.R., 2003. Longitudinal assessment of immature-to-adult ratios in two groups of Costa Rican *Alouatta palliata*. *International Journal of Primatology* 24, 87–101.