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Forest fragmentation and the distribution, abundance and conservation of the Tana river red colobus (*Procolobus rufomitratus*)

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Abstract

Evidence suggests that habitat heterogeneity, disturbance, disease, predation and food resources influence primate population abundance. However, few studies have focused on what habitat factors determine the probability that a primate species will occur in a habitat fragment. We analysed forest habitat and colobus population attributes to determine factors that influenced occurrence and abundance of the critically endangered Tana River red colobus. The probability of colobus inhabiting forests was positively related to the relative amount of habitat edge and canopy tree species composition. Most of the variance in the density of colobus monkeys was explained by basal area of food trees (per ha), basal area per food tree, density of food trees, and basal area per tree for all trees. We conclude that effective conservation of primates in fragmented habitats may require strategies that consider factors that influence both the occurrence of a species and its relative abundance.

Keywords: Habitat quality and fragmentation; Conservation; Primates; Red colobus; Tana river

1. Introduction

In patchy landscapes, the probability of local extinction of a species increases with decreasing patch area and increasing isolation, while the probability of colonization increases with increasing patch size and decreasing patch isolation from other occupied patches (connectivity; Moilanen and Hanski, 1998). This area-isolation paradigm from metapopulation theory is currently a primary focus of the study of species living in fragmented habitats (Hanski, 1999). Conservation strategies based on this paradigm advocate for maintaining suitable metapopulation geometry (i.e. optimal patch size and connectivity; Hanski, 1999). However, increasing evidence shows that habitat quality of fragments has major influences on metapopulation dynamics (Gyllenberg and Hanski, 1997; Hanski, 1999; Fleishman et al., 2002). Because habitat quality, in addition to area and isolation, is important in determining the dynamics of populations living in fragmented landscapes (Fleishman et al., 2002), effective conservation strategies may require much more than just suitable geometry. From a conservation perspective, it is important to understand what habitat variables determine the likelihood of a habitat patch being occupied by the species of interest, because such knowledge can potentially provide managers with more effective guidelines on how to restore degraded habitat.

The Tana River red colobus is the most endangered primate species in Africa (Grubb et al., 2002; Groves, 2001). It is endemic to a unique community of tropical riverine forest patches in a highly fragmented ecosystem in eastern Kenya (Fig. 1). During the last 30 years, the total population of Tana River red colobus has been estimated to number no more than 1300

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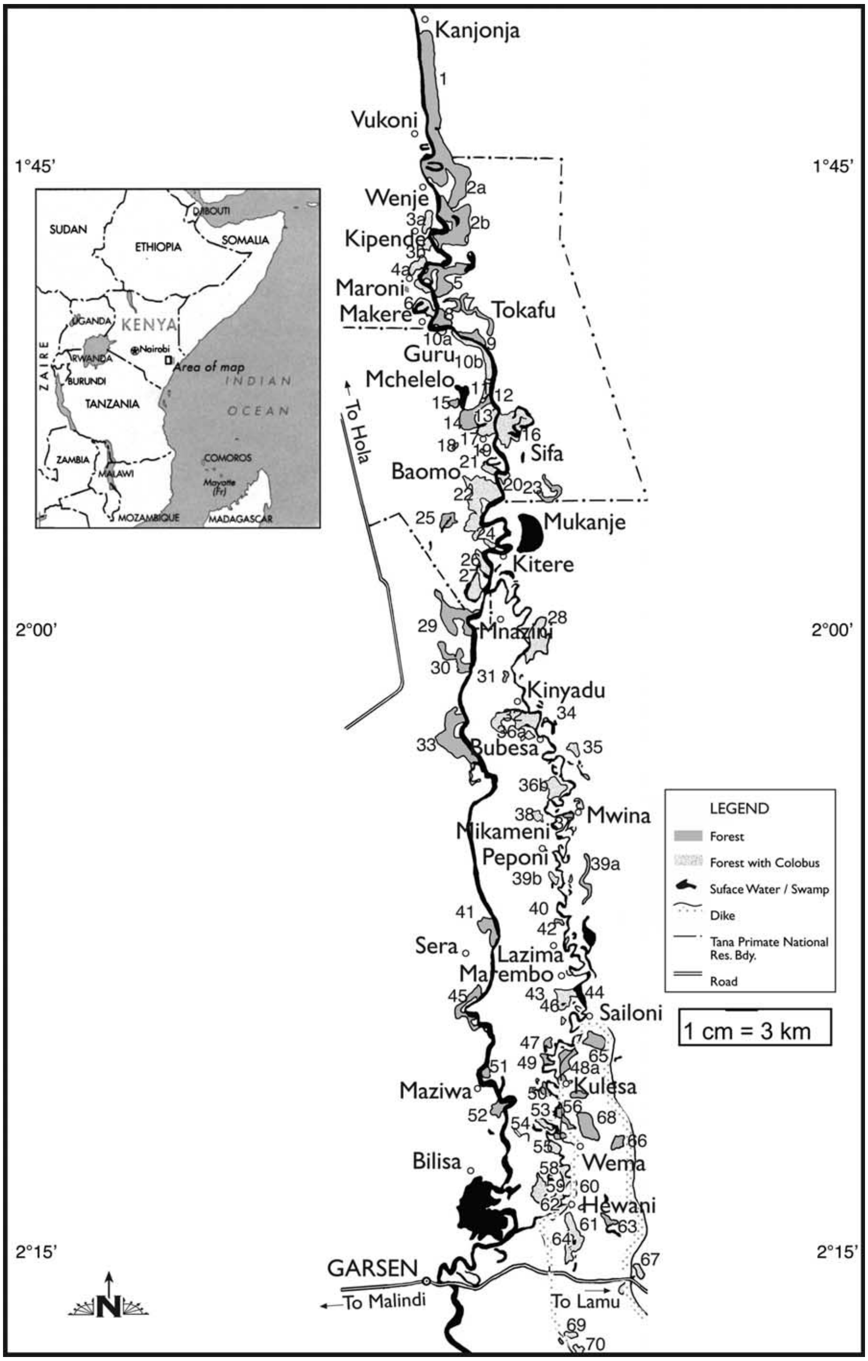

Fig. 1. Distribution of forest patches (numbered) along the Tana River and the location of the Tana River Primate National Reserve (TRPNR). This figure is adapted from Butynski and Mwangi (1994) and World Bank (1996).

individuals (Butynski and Mwangi, 1994; Decker and Kinnaird, 1992), and the mean group size has declined by nearly 50% since the 1970s. Over the 30 years, several censuses of red colobus show a consistent pattern where colobus occupy only half of the available forest patches within their range. It is not understood what factors are responsible for the intermittent distribution of red colobus in forests or what habitat factors influence their abundance across the landscape. Understanding the factors that influence population distribution and abundance can greatly enhance attempts to protect suitable colobus habitat and stop the decline in their population size. Therefore the primary goal of this study was to determine what habitat characteristics influence patch occupancy by the Tana River red colobus, as well as the most important habitat attributes determining the density of colobus and the mean social group size.

The pattern of distribution of primate populations in forest fragments whereby some fragments are occupied while others are not can be the result of two basic processes. Following habitat fragmentation primates may be randomly distributed within fragments resulting in some patches being occupied while others are not (Marsh, 2003). In addition, primates may become locally extinct from patches that were initially occupied due to factors such as inadequate fragment size, insufficient food resources or shortage of critical food sources among other reasons (Marsh, 2003).

Populations that inhabit forest fragments face several consequences. These include altered population density as a result of group size and composition changes (Terborgh et al., 1997; Tutin, 1999); altered dietary and foraging strategies (Johns and Skorupa, 1987; Tutin, 1999); and disrupted gene flow among populations in different fragments (Pope, 1996; Gravitol et al., 2001). Furthermore, the ability of primates to survive in habitat fragments is influenced by home range size, behavioral and dietary plasticity, degree of frugivory in the diet, and the ability of a species to use the matrix (Onderdonk and Chapman, 2000; Silver and Marsh, 2003).

Several primate studies show a high degree of variability in density of primates between sites at local (e.g. Chapman and Chapman, 1999), and regional scales (Ganzhorn, 1992; Oates et al., 1990). These differences in density are attributed to three factors influencing primate population abundance: food availability, predation, and disease (Cowlishaw and Dunbar, 2000; Davies, 1994). Food resource abundance and availability influence demography and social organization in varying ways depending on the particular primate species and the habitat under consideration (Siex and Struhsaker, 1999; Dunbar, 1987; Eisenberg et al., 1972). Red colobus living in gallery forests in semi-arid areas have social groups that are half or less than half the size of the average group size of red colobus living in rain forests (Struhsaker, 1975; Struhsaker and Leland, 1979) and where forest habitat is patchy, smaller forests may contain smaller groups (Struhsaker, 1975; Gatinot, 1978). Siex and Struhsaker (1999) found a higher variation in group size, and lower rates of juvenile recruitment in Zanzibar red colobus (*Procolobus kirkii*) living in agricultural areas where basal area of food trees was lower and habitat fragmentation was higher due to human activities, than in contiguous forested areas.

Although food resource abundance is recognized as an important factor determining population density in primates (Chapman and Chapman, 1999), it is unclear if food resources influence habitat occupancy by primates in fragmented forests (but see Onderdonk and Chapman, 2000; Tutin et al., 1997). Furthermore, testing specific hypotheses on limiting food resources is often complicated by the high dietary flexibility of many primate species (Cowlishaw and Dunbar, 2000). However, colobine monkeys have a highly specialized digestive system that restricts them to a vegetarian diet comprising mainly leaves, seeds and some unripe fruit (Waterman et al., 1988; Oates et al., 1990; Davies, 1994; Davies et al., 1999; Chapman et al., 2002).

Predation pressure on the Tana red colobus is probably very low, because chimpanzees and predatory eagles, two key colobus predators, are not present in the Tana (Struhsaker, 2000a,b), and no hunting of colobus by humans occurs (*personal observation by DNMM*). Parasite infestation and diseases have not been investigated in the population. However, in the more than 30 years that this population has been studied, there are no reports of disease epidemics. Therefore, food abundance, vegetation structure, human disturbance, and spatial characteristics of forests may have a relatively large influence on the distribution and abundance of the colobus population. Significant differences in vegetation characteristics may exist between forest patches that are inhabited by colobus compared to those uninhabited.

We measured colobus monkey density and mean group size along with forest vegetation attributes from July 1999 to August 2001. We applied logistic regression analysis to determine the relationship between habitat attributes and habitat occupancy by colobus, and multiple regression analysis to determine the habitat attributes that best predicted abundance of colobus in forest fragments. We expected that habitat occupancy by colobus would be positively associated with forest area. We also predicted a positive association between the abundance of colobus and the diversity, density, and abundance of food trees (Dunbar, 1987; Medley, 1993; Chapman and Chapman, 1999). Furthermore, we predicted a negative association between colobus abundance and measures of forest habitat disturbance (cut stems) because such activities remove forest resources and possibly lower habitat quality (Medley, 1993). Finally, we expected a positive relationship between colobus abundance and forest patch area as has been demonstrated in several studies on the relationship between animal density and patch area (Connor et al., 2000; Andren, 1994).

2. Methods

2.1. Study design and forest patch sampling protocol

Tana forests are found in the lower floodplain of the Tana River in eastern Kenya occurring in scattered patches of various sizes, on both sides of the river (Fig. 1). We defined “forest” as a wooded area exceeding 1 ha that was composed mainly of trees greater than 10 m in height and with a canopy cover exceeding 50%. The matrix is mainly cultivation, riparian grassland and dry shrubs. These forests are unique because they support a high diversity of plant and animal species, including several endemics, and because they exist in a semi-arid environment (annual rainfall $\leqslant$ 400 mm; Marsh, 1976). The depth of the water table drops off rapidly from the edge of the river, thereby determining the lateral extent of the forests (Hughes, 1990). The forests are a relic of a more continuous rainforest that extended from the Congo Basin to the east coast of Africa during the Pleistocene (Hamilton, 1974). Subsequent climatic drying led to shrinkage and isolation of these evergreen forests and left them confined to the moist riverine area.

There are three major forest vegetation types associated with the floodplain geomorphology (Hughes, 1990; Njue, 1992); an association of evergreen forest species found on well drained (sandy) high levees, a dense growth of forest species on poorly drained low levees, and an association of species found in the transition area between the edge of the forest and the dry bushes beyond the floodplain.

2.2. Habitat analysis

We calculated forest area, perimeter, and area-to-perimeter ratios from a GIS analysis of aerial photographs taken in 1994 and 1996. To capture the range of habitat conditions within the floodplain, we systematically selected 20 forests with colobus groups and 11 forests without colobus at the time of study. We chose forests so that approximately equal areas were sampled east and west of the Tana River, and inside and outside the Tana River Primate National Reserve. Within each forest, we systematically established vegetation belt transects running from the riverbank side directly away from the river towards the far edge of the forest patch (i.e. perpendicular to the river channel). Each belt was 5 m wide, and usually ran for a maximum length of 100 m unless the width of the forest was less than 100 m. The orientation of the transect allowed for a detection of changes along the main environmental gradient in the system, the increasing depth of the water table as one moves away from the river channel in the floodplain (Hughes, 1990). The number of transects sampled in each forest was based on the size of the forest. We sampled three transects in all forests less than 5 ha because three belts is the minimum for a reasonable estimate of variance (Sokal and Rolf, 1981). For forests bigger than 5 ha, we added one belt transect for every 10-fold increase in area since species increase with area logarithmically rather than linearly, making this a more efficient approach than sampling a fixed area of the forests (Gotelli and Colwell, 2001).

In each transect, we collected data for canopy trees that were both at least 10 m in height and 10 cm in diameter at breast height (DBH). Data were collected in 10 m segments (hereafter called plots) along the belt transect. We recorded species identity, height and DBH of each tree in each plot (i.e. for each of the 10 plots per 100 m belt transect), and also measured amount of canopy cover every 20 m by photographing the canopy using a 35-mm lens. The canopy photographs were then digitally analysed to determine percentage canopy cover. Forest disturbance and use by humans was documented by recording the DBH of cut stems or damaged trees on the transect.

2.3. Abundance and structure of colobus groups

Data on colobus groups were collected by systematically surveying forests for primate groups (National Research Council, 1981). 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 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

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 (m^2/ha), stem density (individual trees/ha), and frequency of all tree species (percentage of plots each species was found in), and then computed a relative importance percentage for each species at each study forest (Barbour et al., 1999). We also calculated absolute values for basal area, density and frequency of all species, and relative importance percentage for trees cut or otherwise damaged by humans as a measure of human use of forests, and for tree species important as food sources for the Tana red colobus. The important food tree species were selected from two studies of the Tana red colobus, each conducted over a period of one year (Decker, 1994; Marsh, 1981). These studies computed the contribution of various tree species to the colobus diet via observations during all day group follows. We used the top 13 species because they constituted more than 80% of feeding records in each study (Decker, 1994; Marsh, 1981).

We used detrended correspondence analysis (DCA) ordination to summarize the vegetation community pattern and to determine the major environmental gradient influencing vegetation community types (Hill and Gauch, 1980). The DCA ordination groups forests with similar species composition and abundance (i.e. they are closer together in the ordination plot) with dissimilar forests located farther apart from each other. Therefore DCA ordination axes, scaled in units of beta diversity (species turnover between sites), show how different samples are from each other in species composition and abundance (ter Braak, 1995), and measure the length of ecological gradients (Legendre and Legendre, 1998). The arrangement of study sites on the first axis of a DCA ordination corresponds to the most important compositional (and therefore environmental) gradient in the system. We therefore used axis 1 scores of the DCA as a measure of the forest tree species composition gradient (Gauch, 1982). The ordination was done using PC-ORD version 4 (McCune and Mefford, 1999).

Vegetation structural attributes (e.g. basal area, density and canopy cover and other derived measures), measures of species diversity, DCA axis 1 scores, and colobus demographic attributes (density and mean group size) were summarized for each forest and used on a per forest basis in all subsequent statistical analyses.

2.5. Data analysis

We used stepwise multiple logistic regression analysis (Hosmer and Lemeshow, 2000) to determine important habitat attributes influencing the probability of a forest being occupied by colobus, and stepwise multiple regression analysis to determine habitat attributes that predicted variance in colobus density and mean group size (Kleinbaum et al., 1998). Colobus density and mean group size were used as response variables in turn to screen the pool of habitat attributes as potential predictors of population abundance (Kleinbaum et al., 1998). All analyses were done using SAS version 8.1 for Windows (SAS Institute, Cary, NC).

3. Results

3.1. Vegetation community patterns

We sampled a total area of 49,850 m^2 in 109 belt transects distributed in 31 study forest patches, and enumerated 70 tree species in 34 families. We identified three community types from the DCA plot of the forest stands (Fig. 2) coinciding with the major landforms found on the floodplain (Hughes, 1990); sandy levees closest to the river channel (low DCA axis 1 scores), low levees in intermediate position (intermediate DCA axis 1 scores) and high floodplain that is farthest from the river channel (high DCA axis 1 scores). This corresponds with vegetation community types identified by previous vegetation studies (Hughes, 1990; Njue, 1992).

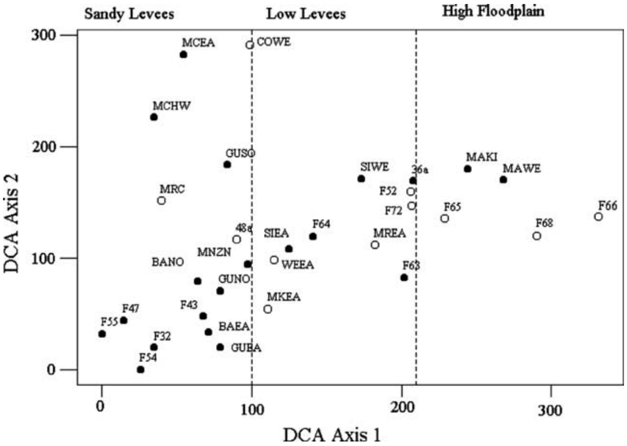

Fig. 2. Detrended correspondence analysis (DCA) plot of study forests in the Tana River Floodplain. Dotted lines delineate vegetation community types corresponding to those identified by Hughes (1990) and Njue (1992).

3.2. Probability of occupancy and population abundance

We recorded 613 red colobus monkeys in the 55 social groups that we observed in 20 forest patches with colobus (Table 1). This represents close to 50% of the total population estimated for this species in 1994 (Butynski and Mwangi, 1994). The mean group size was 10.5 animals, and groups ranged from 4 to 31 animals. Mean density of colobus monkeys (individuals per ha) was 0.80 (range 0.01–3.3), and mean density of social groups (groups per ha) was 0.08 (range 0.03–0.21; Table 1).

Occupancy of forests by colobus was predicted by relative amount of forest edge (measured as area-to-perimeter ratio) and axis 1 scores of the DCA (logistic regression; likelihood ratio test, df = 2, $\chi^2 = 6.9$, $p = 0.03$, $R^2 = 0.29$). None of the other habitat attributes predicted occupancy (residual chi-square test

Table 1

Descriptive statistics of colobus group size, density of animals and social groups in the Tana forests

Variable	*N*	Mean	SEM	Range
Group size	55 groups	10.49	(0.69)	4.0–31.0
Density of colobus monkeys	20 forests	0.80	(0.19)	0.01–3.28
Density of colobus groups	20 forests	0.08	(0.01)	0.03–0.21

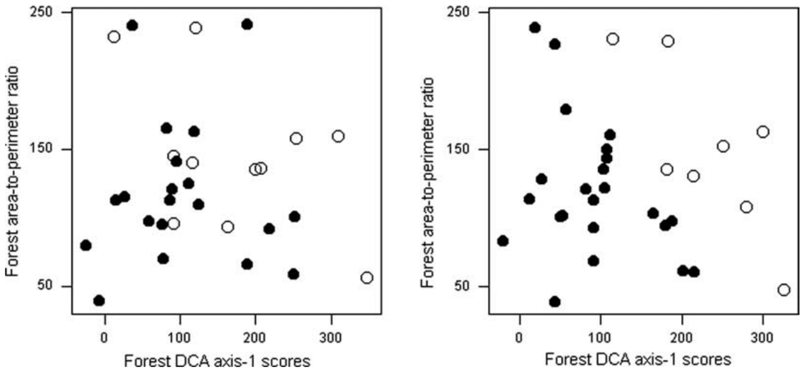

Fig. 3. Forest area-to-perimeter ratios plotted against forest DCA axis 1 scores; the number of forests occupied by colobus (solid circles), decreases with increasing area-to-perimeter ratios and DCA axis 1 scores. The panel on the left shows forests observed in the field as occupied or not, and the panel on the right shows model based predictions of occupancy (a model based prediction probability of $\geqslant 0.5$ resulted in a prediction of "occupied").

Table 2
A classification table of forests correctly classified as occupied or not, by colobus by the logistic regression model

	Predicted		
	Occupied	Unoccupied	Percent correct
Observed			
Occupied	18	2	90%
Unoccupied	5	6	54%
Overall classification accuracy			77.42%

Forests with a probability $\geqslant 0.5$ were considered occupied.

df = 19, $\chi^2 = 18.64$, $p = 0.48$). The probability of forest occupancy by colobus tended to be positively associated with the relative amount of edge to area (i.e. decreasing area-to-perimeter ratio; $\chi^2 = 3.41$, df = 1, $p = 0.07$) and the DCA axis 1 scores; ($\chi^2 = 3.39$, df = 1, $p = 0.07$, Fig. 3). Using the classification rule that a model based predicted probability of $\geqslant 0.5$ implied a forest was occupied, 77.4% of the forests were correctly classified by this model as being occupied or not (Table 2).

Colobus monkey density was positively associated with absolute basal area of food trees, and negatively associated with absolute basal area per food tree, absolute density of food trees and mean basal area per tree (Table 3). These factors jointly accounted for 88% of the variance in colobus monkey density. However, absolute basal area of food trees alone accounted for 73% of the variance in the density of colobus (Table 3). Mean group size was positively associated with absolute basal area of food trees, and was negatively associated with absolute basal area of all trees and area-to-perimeter ratio of forests (Table 3). Overall, the model was highly significant (Table 3), but absolute basal area of food trees and absolute basal area of all trees were the most important factors determining mean group size and jointly accounted for 51% of the variance in mean group size (Table 3).

3.3. Comparison between occupied and unoccupied forests

There were few differences in habitat attributes between forests with colobus and those without colobus. Forests with colobus had significantly lower DCA axis 1 scores, and showed a trend towards a higher absolute basal area of food trees than those without colobus ($t = 2.14$, $p = 0.046$, df = 18, $t = -1.84$, $p = 0.076$, df = 28 respectively).

4. Discussion

On axis 1 of the DCA ordination, forests are spread along a moisture availability gradient (Fig. 2). Forests with low axis 1 scores are dominated by species found on well-drained sandy levees closer to the river channel (mesic sites) and these had the highest probability of being occupied. Intermediate axis 1 scores correspond to forests in low lying parts of the floodplain that have a high water table but with poorly drained clay soils (Hughes, 1990). Xeric sites are the transition zone between the forested floodplain and the open plains with a deep water table and are the forests with high axis 1 scores dominated by species adapted to low moisture conditions, farthest from the river channel (Hughes,

Table 3
Stepwise multiple regression analysis of habitat attributes determining colobus density and mean group size (df = 27, for all cases)

Variables	Coefficient	SE	F	p	Partial r^2	Model R^2	F	p
Colobus density (animals/ha)								
Absolute basal area of food trees (m^2/ha)	0.053	0.006	67.58	0.00	0.73	0.73	68.86	0.00
Absolute basal area per food tree (m^2/ha)	−3.059	0.569	28.88	0.00	0.05	0.78	5.47	0.02
Absolute density of food trees (trees/ha)	−0.009	0.002	20.52	0.00	0.06	0.83	8.51	0.01
Absolute basal area per tree (m^2/ha)	−3.284	1.041	9.96	0.00	0.05	0.88	9.96	0.00
Mean group size								
Absolute basal area of food trees (m^2/ha)	0.156	0.043	13.23	0.00	0.37	0.37	14.93	0.00
Absolute basal area of all trees (m^2/ha)	−0.103	0.038	7.48	0.01	0.15	0.52	7.43	0.01
Forest area to perimeter ratio (m^2/ha)	−0.035	0.015	5.31	0.03	0.04	0.61	2.60	0.12
Side of river bank (east/west)	−3.299	1.606	4.22	0.05	0.04	0.65	2.64	0.12

1990; Njue, 1992). While the ultimate explanation for the distribution of different forest communities on the floodplain could be moisture availability, the proximate causes of the species distributions and dominance may be driven by other factors. Particularly, species' shade tolerance can be an important factor determining the succession sequence of species at sites and therefore the observed species composition at study forests (Curtis, 1987).

The fact that probability of forests being occupied by colobus declined, in part, with increasing axis 1 scores of the DCA (i.e. increasing distance from the river) shows that forest tree species composition may be an important factor determining if forests were occupied by colobus. Forests farthest from the channel may be different in tree species composition or have lower abundances of food resource species compared to those closer to the channel. These differences may be due to limited amounts of moisture, as a result of a deeper water table, possibly making forests that are far from the river less suitable as colobus habitat. This may explain why density of food trees was inversely related to DCA axis 1 scores ($R^2 = 0.25$, $p = 0.00$) and was the only habitat attribute related to axis 1 scores of DCA.

The increasing probability of occupancy with increasing relative amount of habitat edge (i.e. decreasing area-to-perimeter ratio) suggests that colobus monkeys may prefer more disturbed forests. This conjecture is supported by studies on the impacts of disturbance caused by selective logging on primate populations in some parts of Africa and Asia. Forest leaf production increases after disturbance (Johns, 1988), and young leaves typically have fewer chemical defences, are more digestible, and have higher nutrition value for primates (Coley and Barone, 1996). This finding is also consistent with other studies that have found a positive correlation between the percentage of foliage in the diet and survival of some primates in disturbed habitats (Johns and Skorupa, 1987). For example, black and white colobus (*Colobus guereza*) respond positively to logging (Plumptre and Reynolds, 1994; Struhsaker, 1997) while the Uganda red colobus (*C. badius*) seems to thrive in disturbed forest habitat (Onderdonk and Chapman, 2000).

Studies have shown that biomass of colobine monkeys in Africa and Asia is positively related to the ratio of protein-to-fibre, which is an index of mature leaf quality (Davies, 1994; Oates et al., 1990). It is also associated with the abundance of leguminous trees in their habitat in Asia (Davies, 1994) but not in Africa (Davies et al., 1999; Chapman et al., 2002), and Chapman and Chapman (1999) reported that it is related to cumulative basal area of food trees at Kibale (Africa) if they removed one anomalous study site from the analysis. Therefore, we expected both colobus density and group size to be positively associated with diversity and abundance of trees. Colobus density was positively associated with absolute basal area of food trees, but was negatively associated with basal area per food tree, absolute density of food trees and basal area per tree (Table 3). This implies that a high density of food trees per hectare cannot support a large number of animals because individual trees would not be very large and therefore have low basal area coverage. Conversely, a few very large trees (high basal area per tree) might not favour high colobus abundance because this would increase competition among foraging animals crowded in a few large trees as shown by Dunbar (1987) for black-and-white colobus (*Colobus guereza*) living in another patchy environment. However, these latter negative relationships account for a small amount of the variance explained by the model, only 16%, compared to basal area of food trees, which alone accounts for 73% of the variance in the density of colobus monkeys. Similarly, mean group size was positively related to absolute basal area of food trees, but was negatively related to absolute basal area of all trees (Table 3). Thus basal area of food trees is the single most important determinant of colobus population abundance in terms of both density and average group size.

We found no evidence for the expected positive relationship between abundance of colobus and the size of habitat patches (Connor et al., 2000). The enemies and movement hypothesis predicts a positive correlation between population density and patch area. It postulates that if habitat quality is positively correlated with patch area and predation risk is lower in larger patches, then animals are less likely to disperse from larger patches and thus population density remains high there (Matter, 1997; Møller, 1995; Foster and Gaines, 1991). Furthermore, ongoing fragmentation should lead to negative area–density relationships as survivors crowd into remaining reduced forest habitat (Bierregaard et al., 1992; Hagan et al., 1996). However, with time, positive correlations between population density and patch area are more likely to occur in highly fragmented landscapes because extinction probability is usually higher on smaller patches due to Allee effects (Andren, 1994; Connor et al., 2000).

The enemies and movement hypothesis is not likely to apply to the Tana River colobus population because predation pressure is probably relatively low, and we did not find any correlation between habitat quality and patch size (e.g. linear regression of basal area of food trees against forest area; $F = 0.78$, $p = 0.38$, $R^2 = 0.03$). Nevertheless, fragmentation as a causal mechanism for a significant density–area relationship could be a possibility in Tana because in addition to natural fragmentation of forests, significant amounts of human induced fragmentation continue to occur. For example, Decker (1994) reported that extensive forest fragmentation occurred in the Tana forests in the 1960s and 1970s due to a river course change and clearing of forest by humans for cultivation.

The lack of a positive relationship between colobus population density and patch area suggests that density of colobus monkeys in the Tana forests could be a random sample from original forest habitat (Connor and McCoy, 1979). However, patterns of habitat occupancy do not support the random sample hypothesis as a potential explanation for the lack of a correlation between colobus density and patch size. Habitat occupancy as predicted by the logistic regression model explained a modest, but significant, amount of variance ($R^2 \approx 0.30$, $p = 0.03$) and correctly classified 77.4% of forests as occupied or not by colobus (Table 2). Based on model predictions, we found that at least 4 of the 11 study forests not occupied by colobus at the time of this study were probably suitable for occupation as they had a predicted probability of occupancy greater than 50%. Thus there may be local extinctions of colobus in patches without immediate recolonization. Conversely, 5 of the 20 forests occupied by colobus at the time of this study had a predicted probability of occupancy less than 50%, implying that these forests were probably not as suitable for occupation as others and indicating the possibility of source–sink dynamics in the system (Pulliam, 1988; Fig. 3).

The observation that there are “suitable” unoccupied forests and “unsuitable” occupied forests suggests that the population of the Tana River red colobus may show metapopulation dynamics (Hanski, 1999). Therefore, the ability of colobus monkeys to move between habitat patches may play a key role in determining their distribution in the system. Yet, two important factors may hinder dispersal between forests by red colobus. Tana colobus are almost exclusively arboreal (Marsh, 1978) and the intervening matrix between forest fragments can be cultivation and human settlement, wooded bush-land or riparian grassland. Thus these habitat types in the intervening matrix may have different influences on ability of colobus to colonize forest patches. An important area of further research is to determine the role of the intervening matrix in influencing probability of forest occupancy and how this interacts with the other factors as presented in this study.

For most forest primates, habitat alteration and destruction occur through forest clearing for cultivation, commercial timber harvesting and extraction of non-timber forest products (Mittermeier et al., 2002). In many parts of the world where primates are found, these activities are so severe that they threaten many primate species with extinction (Mittermeier et al., 2002). Therefore, there is an urgent need for a clear understanding of specific habitat attributes that are key in determining population distribution and abundance in order to develop effective conservation measures. Particularly, for timber and non-timber forest uses, such knowledge can be used to focus harvest strategies to avoid removing tree species and/or impacting attributes most important to primate species. Where habitat is already altered, restoration and enrichment programs can be developed. However, such a conservation strategy can only be effective if the habitat attributes identified are easy to measure and account for a large amount of variance in the population abundance.

We believe that the strong relationship between colobus abundance and basal area of food trees we have reported here can serve as an important conservation tool. Forest fragmentation and degradation continues in the Tana forests due to increasing demand for forest products (e.g. selective removal of large trees for canoe building) and forest clearing for farmland from an expanding human population (Mbora and Wieczkowski, 2001). Additionally, upstream dams on the Tana River have altered river flow dynamics (Hughes, 1990). As these dynamics are necessary for forest regeneration and maintenance, this will probably cause further habitat decline. As some of the forests have been reduced into smaller patches, and their structure and composition altered, their suitability as primate habitat may have decreased, as may have the likelihood of colobus monkeys to disperse to more isolated suitable patches. Therefore, it is important to know the habitat attributes that determine occupancy of forest patches and the abundance of colobus as such knowledge can be applied in a habitat restoration program, in curbing human activities that could cause further habitat deterioration with specific negative impacts on the red colobus and to determine the effectiveness of current conservation measures.

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