

RESEARCH ARTICLE

Ecological Correlates of Abundance in the Tana Mangabey (*Cercocebus galeritus*)

JULIE WIECZKOWSKI*

Department of Anthropology, University of Georgia, Athens, Georgia

I investigated the ecological correlates of abundance in the Tana mangabey (*Cercocebus galeritus*), one of the world's most endangered primates, with the goal of recommending management strategies. I systematically selected 31 forest fragments throughout the mangabey's 60-km distribution along the lower Tana River in southeastern Kenya. Within the 31 fragments, I measured vegetation structure, food abundance, and human forest product use in 107 belt transects, and conducted 370 mangabey surveys. I used a weighted multiple regression analysis to determine whether there was a dependence between the selected forest attributes and the mean number of mangabey groups per fragment. Fragment area and density of trees ≥ 10 cm diameter at breast height (DBH) were the only variables that significantly correlated with the variation in mangabey abundance. No additional variables were significant when the analysis was limited to forest fragments inside the Tana River Primate National Reserve (TRPNR) or to fragments outside the TRPNR. When I estimated the resources available before recent human forest product use by adding nonharvested and harvested variables, the total basal area of the top 15 food species became significant. This was only within the TRPNR, however. Management, therefore, should focus on increasing forest area, density of trees ≥ 10 cm DBH, and coverage of food trees throughout the mangabey's distribution. Solutions must be found for the problem of forest clearing, and forest product use must be better managed to protect the habitat of this critically endangered primate. The significance of food abundance only within the TRPNR suggests a need to collect dietary data from mangabey groups in fragments toward the southern limit of the mangabey's distribution, where plant species composition differs from that in fragments in which dietary data have been previously collected. *Am. J. Primatol.* 63:125–138, 2004. © 2004 Wiley-Liss, Inc.

Contract grant sponsor: Wildlife Conservation Society; Contract grant sponsor: Margot Marsh Biodiversity Fund; Contract grant sponsor: Primate Action Fund, Conservation International; Contract grant sponsor: Primate Conservation, Inc.

*Correspondence to: Julie Wieczkowski, Department of Anthropology, State University of West Georgia, Carrollton, GA 30118. E-mail: juliewhiz@yahoo.com

Received 3 May 2003; revised 4 April 2004; revision accepted 18 May 2004

DOI 10.1002/ajp.20046

Published online in Wiley InterScience (www.interscience.wiley.com).

Key words: forest attributes; management; endangered primate; forest product use; habitat needs; forest fragments

INTRODUCTION

The most serious threat to the majority of threatened nonhuman primates is habitat destruction [Mittermeier & Konstant, 2002]. It is therefore critical to understand the vegetation attributes that support primates. This knowledge can be used to recommend management and conservation strategies [Estrada & Coates-Estrada, 1996; Medley, 1993b; Stevenson, 2001]. In this study, I investigated the ecological correlates of abundance in the Tana mangabey (*Cercocebus galeritus*) with the goal of recommending management strategies.

Based on MacArthur and Wilson's [1967] island biogeography theory, a larger forest should support a greater abundance of primates. In previous studies, the area of the forest fragment was correlated with the number of *Alouatta palliata* individuals in 126 forest fragments in Los Tuxtlas, Mexico [Estrada & Coates-Estrada, 1996], and the total number of *Procolobus badius* and *Cercocebus galeritus* groups in 10 fragments in Tana River, Kenya [Medley, 1993b].

Several studies have found primate abundance to be correlated with the availability of the species' primary or keystone resource [Medley, 1993b; Skorupa, 1986]. In a study of 30 sites across the neotropics, Stevenson [2001] determined that the biomass of large atelines (*Ateles* spp., *Brachyteles arachnoides*, and *Lagothrix lagotrica*) was positively correlated with the basal area of figs, which are an important resource in the dry season. In addition, the biomass of the seed predators (*Cacajao calvus*, *Chiropotes satanas*, and *Pithecia* spp.) was positively correlated with the basal area of *Eschweilera*, their preferred diet species. Examining a longer list of important diet species, Skorupa [1986] found that the abundance of *Colobus badius* across three plots in Kibale National Park, Uganda, was positively correlated with the total basal area of trees that contributed the top 80% of their annual diet. Balcomb et al. [2000] and Chapman and Chapman [1999] also found positive correlations between primate abundance and availability of top diet species.

Various forest structural attributes have also been found to be important correlates of primate abundance. For many primates, these important attributes include the number and size of trees [Medley, 1993b; Ross & Srivastava, 1994; Skorupa, 1986], the percentage of canopy cover [Skorupa, 1986], and the size of cut, dead, or damaged trees [Medley, 1993b].

The Tana mangabey (*Cercocebus galeritus*) is endemic to forest fragments along a 60-km stretch of the lower Tana River in Kenya. The last reliable estimate of the population was only 1,000–1,200 individuals [Butynski & Mwangi, 1994]. Habitat loss is the greatest threat to the mangabey. In recent years, there has been a 30% loss in forest area, and an increase in forest degradation within the mangabey's distribution [Wieczkowski & Mboru, 2000]. Consequently, the Tana mangabey is classified as critically endangered [Butynski et al., 2000] and as one of the world's top 25 most endangered primates [Mittermeier & Konstant, 2002]. Conservation of this endangered primate would be furthered by an understanding of the forest attributes that support its population.

Medley [1993b] looked at 10 forest attributes in order to determine what constitutes “suitable” habitat for the mangabey within the Tana River Primate National Reserve (TRPNR). She found that mangabey abundance (number of groups and/or number of individuals) was positively correlated with the mean canopy height, *Phoenix reclinata* density, and forest area-to-perimeter ratio. In addition, abundance was negatively correlated with forest disturbance and intraforest heterogeneity. I broadened Medley’s [1993b] investigation, addressing gaps in our knowledge of the ecological correlates of mangabey abundance. Most importantly, I included forest fragments on the east bank of the Tana River and to the south of TRPNR. There has been no previous systematic work in these fragments (but see Mbora [2003]). Forest composition differs between fragments inside and outside the TRPNR [Medley, 1992], suggesting that forest structure and human impact may differ as well. The results of this study allowed me to compare these forest subsets and determine whether the ecological correlates of mangabey abundance differed between them. I also accounted for movement of mangabey groups among the forest fragments to reflect abundance better in each fragment.

Regarding the attributes investigated, I measured the abundance of food species that are important to the mangabey. In a previous study, Medley [1993b] combined colobus and mangabey food species into one measure, and also combined trees that were cut, dead, or damaged by animals into one measure of forest disturbance. Because human forest product use has been extensive in this region since 1994 [Wieczkowski & Mbora, 2000], and continued to be so during the data-collection period, I included a specific measure of human forest product use. The recent extreme forest product use also indicates that there may be a “transient time” between habitat degradation and its effect on the mangabey population. This transient time can be defined as “the time it takes for a population to return to population-dynamic equilibrium...following a perturbation in the environment” [Ovaskainen & Hanski, 2002]. I attempted to remove this transient time from the current analysis. I estimated the resources that were available before the recent disturbance by combining nonharvested and harvested basal areas into single composite variables. I then reanalyzed the relationship between mangabey abundance and the forest attributes using these composite variables.

In the research presented here, a number of important factors identified in the primate literature were investigated regarding their associations with Tana mangabey abundance. I predicted there would be a positive association between mangabey abundance and fragment area. Considering that the mangabey is a forest primate, I predicted a positive association between mangabey abundance and the structural measures of density of trees, mean tree height, tree basal area, and area of canopy cover. I also predicted positive associations between mangabey abundance and the basal area of the mangabey’s top 15 food species, and of *Phoenix reclinata* and of *Ficus sycomorus*. The latter two species are considered “critical” resources [Kinnaird, 1990, 1992]. *P. reclinata* is the mangabey’s primary food species, and fruits when other species do not, whereas the fruit of *F. sycomorus* is available year-round. Finally, there is a high degree of resource use overlap between humans and mangabeys, such as for the palm *P. reclinata* [Home-wood, 1976; Kahumbu 1992; Kinnaird, 1990; Medley 1993a]. I therefore predicted negative associations between mangabey abundance and the basal area of harvested trees and of harvested *P. reclinata*.

MATERIALS AND METHODS

Study Area

The study was undertaken within the 60-km distribution of the Tana mangabey along the lower Tana River, Kenya (1°40' to 2°15' S, 40°07' E) (Fig. 1). The lower Tana River supports roughly 62 forest fragments [Butynski & Mwangi, 1994] (Mbora, unpublished results and personal observation). These are classified as floodplain forest, and depend on the Tana River's processes of flooding and nutrient recharge, and the height of the groundwater table [Hughes, 1990], rather than local precipitation. In fact, the lower Tana River is an arid/semi-arid area that receives a mean annual precipitation of 493 mm (averaged across 4 years at Mchelelo Research Camp [Decker, 1989; Njue, 1992] (Marsh, unpublished results).

The forests support more than 57 mammal species, 260 bird species, and 175 woody plant species [Andrews et al., 1975; Medley, 1992]. The forests are especially important for primate conservation because they provide a habitat for eight nonhuman primate species: the Tana River red colobus (*Procolobus rufomitratus*), Tana mangabey, Sykes monkey (*Cercopithecus mitis albotoxatus*), vervet monkey (*Cercopithecus aethiops pygerythrus*), yellow baboon (*Papio c. cynocephalus*), Zanzibar galago (*Galago zanzibaricus*), Senegal galago (*G. senegalensis*), and Garnett's galago (*Otolemur garnettii*) [Butynski & Mwangi, 1994].

Forest Attribute and Mangabey Abundance Data

I collected data from August 1998 to November 2001 in 31 forest fragments (size range=4.8–408 ha; Fig. 1). I classified the fragments according to the following characteristics: with or without mangabeys, west or east bank, and inside or outside the TRPNR (Table I). I made an attempt to sample each category proportionally.

I collected forest-attribute data in collaboration with a concurrent study on the Tana River red colobus, and used methods developed for that study [Mbora & Meikle, 2004]. In each study fragment, I randomly established belt transects that were 5 m wide and 100 m long [Brower et al., 1998]. These belts were placed perpendicular to the river so that I could sample along the gradient of groundwater level, which is an important determinant of forest species composition and structure [Hughes, 1988]. I sampled three transects in fragments of <5 ha. I sampled an additional belt for every 10-fold increase in fragment area. This is preferable to sampling a fixed percentage of each fragment, because the number of species increases logarithmically with area [Lomolino et al., 1989].

Within each belt transect, I recorded the species, height, and diameter at breast height (DBH) of each tree ≥ 10 cm DBH. Mangabeys spend equal amounts of time in the subcanopy layer and the canopy layer [Homewood, 1976], so by measuring trees ≥ 10 cm DBH, I was able to sample both forest layers. I estimated the heights of trees by sight to the nearest meter, and measured DBH with a DBH tape to the nearest 10th of a centimeter.

Fig. 1. The 60-km distribution of the Tana mangabey (*Cercocebus galeritus*) along the lower Tana River, Kenya, showing the location of the Tana River Primate National Reserve (TRPNR), forest fragments, and study forest fragments. Map adapted from Mbora and Meikle [2004].

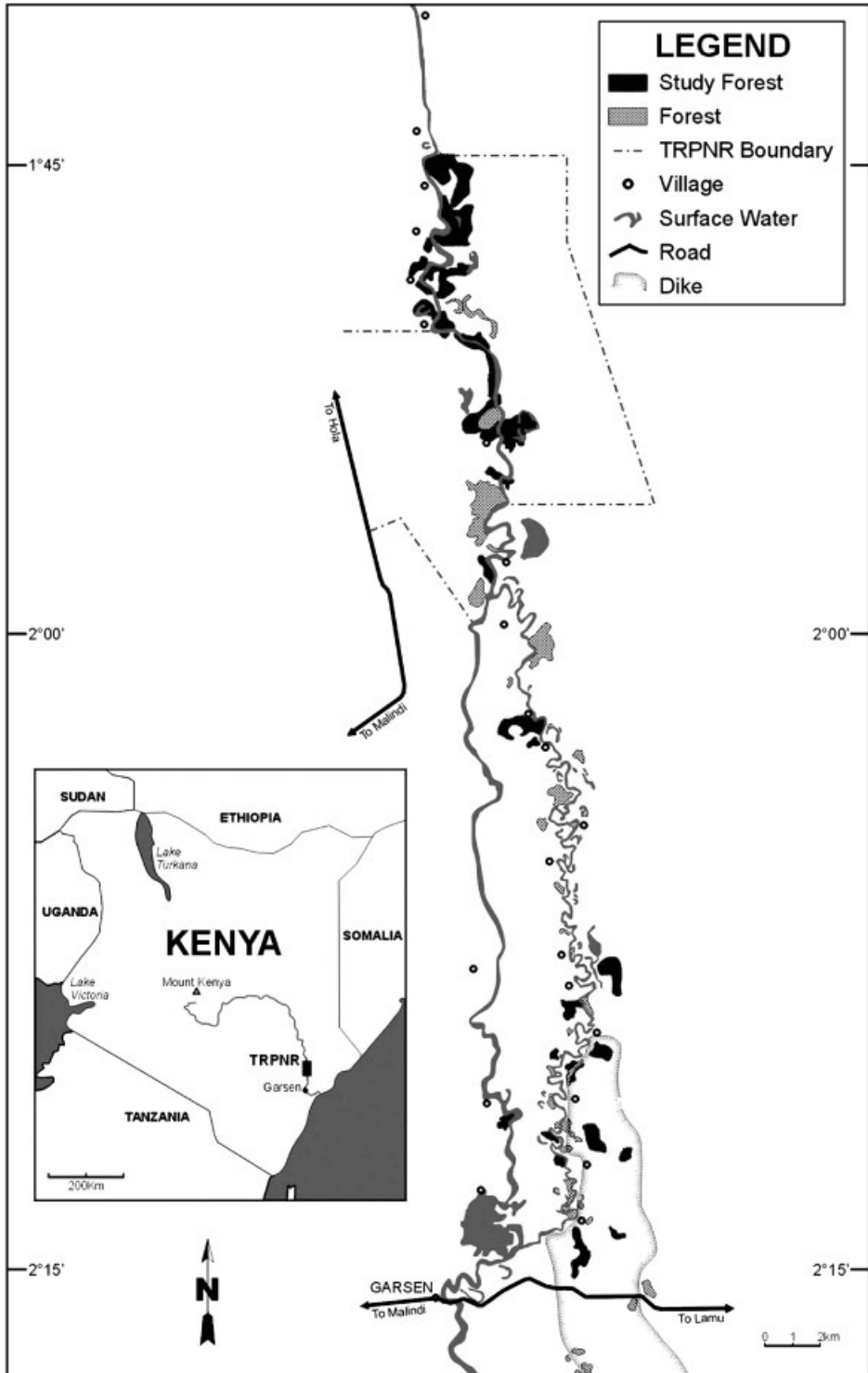


TABLE I. Distribution of Forest Fragments (N) and Study Forest Fragments (n) Inside and Outside the Tana River Primate National Reserve

	West Bank				East Bank				Total	
	Inside		Outside		Inside		Outside		N	n
	N	n	N	n	N	n	N	n		
With mangabeys	11	7	9	5	7	7	13	7	40	26
Without mangabeys	1	1	12	4	1	0	8	0	22	5
Total	12	8	21	9	8	7	22	7	62	31

TABLE II. Top 15 Food Species of the Mangabey, Listed in Alphabetical Order

Species	Family
<i>Acacia robusta</i>	Mimosaceae
<i>Alangium salviifolium</i>	Alangiaceae
<i>Aporrhiza paniculata</i>	Sapindaceae
<i>Borassus aethiopum</i> ^a	Palmae
<i>Diospyros mespiliformes</i> ^a	Ebenaceae
<i>Ficus natalensis</i>	Moraceae
<i>Ficus sycomorus</i>	Moraceae
<i>Hyphaena compressa</i> ^a	Palmae
<i>Mimusops fruticosa</i>	Sapotaceae
<i>Oncoba spinosa</i>	Flacourtiaceae
<i>Pachystela msolo</i>	Sapotaceae
<i>Phoenix reclinata</i> ^a	Palmae
<i>Polysphaeria multiflora</i>	Rubiaceae
<i>Saba comorensis</i>	Apocynaceae
<i>Sorindea madagascariensis</i> ^a	Anacardiaceae

^aDioecious species: only half the basal area was used to calculate the variables "basal area of the top 15 food species" and "basal area of *P. reclinata*."

I generated a list of the mangabey's top 15 diet species by calculating the average percent contribution (to total feeding records) of each plant species in the diets of six mangabey groups [Homewood, 1976; Kinnaird, 1990] (Wieczkowski, unpublished data) (Table II). Three of the top 15 food species (*Saba comorensis*, *Oncoba spinosa*, and *Polysphaeria multiflora*) reproduce at sizes of < 10 cm DBH. For these species, I recorded individuals of < 10 cm DBH that showed evidence of reproduction (fruits, flowers, or the visible remains thereof). For these individuals, I used an average of 8 cm DBH when I calculated the basal area.

Phoenix reclinata, another top diet species, can be separated into four size classes [Kinnaird, 1990]. Reproductive individuals are of size classes 3 (obvious trunk < 2 m tall) and 4 (obvious trunk \geq 2 m tall). I therefore recorded individuals in those size classes. It is difficult to measure the DBH of every *P. reclinata* stem, because it grows in tight clusters. For those individuals I could not measure, I used an average of 15.3 cm DBH when I calculated the basal area.

I identified cut stems of \geq 10 cm diameter and measured the diameter at the cut. This measurement served as an estimate of the basal area lost to harvesting. *Phoenix* individuals in size classes 3 and 4 that had suffered \geq 50% removal of the fronds or topping of the stem were recorded as harvested. It is only near-complete

removal (50–100%) of *P. reclinata* fronds and cutting of the trunk that affects reproductive potential [Kinnaird, 1990]. A summary of the forest attributes measured, and the calculations performed to compute the independent variables based on the above data are presented in Table III.

To measure the canopy cover, I took a black and white photograph of the canopy every 20 m along each transect and continuing to the edge. I digitally analyzed the photos to calculate the area of canopy cover per ha. In addition, I estimated forest fragment areas from 1994 and 1996 aerial photographs of the lower Tana River, using ArcInfo 8.2 and ArcView GIS version 3.2.

I estimated the resources available before the recent disturbance by combining nonharvested and harvested basal areas into single composite variables. I added “basal area of trees” and “basal area of harvested trees” to estimate “total basal area of trees.” I also added “basal area of *P. reclinata*” and “basal area of harvested *P. reclinata*” to estimate “total basal area of *P. reclinata*.” In addition, I estimated the predisturbance “density of trees,” “basal area of the top 15 food species,” and “basal area of *F. sycomorus*” by including harvested individuals. These five new variables replaced the original seven variables in subsequent analyses.

I conducted surveys in each fragment to sample the average number of mangabey groups that were using a fragment. Because some mangabey groups include more than one fragment in their home range [Homewood, 1976; Kinnaird, 1990; Wieczkowski, 2003], the average number of mangabey groups is the most suitable measure of the abundance a single fragment supports. I made an attempt to survey each fragment on a monthly basis, since preliminary observations of several groups suggested that their movement between forest fragments was seasonal (personal observation). Because of the small size of the majority of the study fragments, the surveys were conducted by a small team that moved together. We systematically searched fragments by moving along compass directions and transects 100–200 m apart. The number of transects varied from one to six, depending on the size of the forest fragment. This is a modification of the quadrat census method [National Research Council, 1981], which is the standard method for censusing Tana primates [Butynski & Mwangi, 1994; Kahumbu & Davies, 1993; Marsh, 1986]. Surveys were typically undertaken early in the morning (0630–1000 hr) or late in the afternoon (1400–1700 hr), when the mangabeys are most active and vocalizing. I divided the number of groups seen during all surveys in a fragment by the number of surveys undertaken in that fragment for the dependent variable “mean number of mangabey groups per fragment.”

Analysis

To meet the assumption of a linear relationship with the dependent variable [Zar, 1984], I square-root-transformed the following variables: “fragment area,” “basal area of trees,” “area of canopy cover,” “basal area of the top 15 food species,” “basal area of *F. sycomorus*,” “basal area of harvested trees,” “total basal area of trees,” “total basal area of the top 15 species,” and “total basal area of *F. sycomorus*.”

To determine whether forest structure, mangabey food resources, and human forest product use differed among the 15 fragments inside the TRPNR and the 16 outside, I compared the mean values of each forest attribute between these two subsets with two-tailed *t*-tests (if the data were normally distributed) and Mann-Whitney tests (if the data were not normally distributed).

TABLE III. Forest Attribute Measurements and the Calculations Performed to Compute the Independent Variables Used in the Multiple Regression Analysis*

Measurement	Calculation	Variable
Heights of trees and <i>Phoenix reclinata</i> class 4 stems <50% harvested	Added and divided by number measured	Mean tree height for fragment
Trees and <i>P. reclinata</i> class 4 stems <50% harvested	Counted and divided by number of hectares sampled	Density of trees per hectare
DBH of trees and <i>P. reclinata</i> class 4 stems <50% harvested	Converted to basal area, ^a added, and divided by number of hectares sampled	Basal area per hectare
DBH of individuals (≥ 10 cm DBH) of top 15 food species, <i>P. reclinata</i> class 3 and 4 stems <50% harvested, and reproductive individuals of <i>Polyphaeria multiflora</i> , <i>Oncoba spinosa</i> , and <i>Saba comorensis</i>	Converted to basal area, ^a added, and divided by number of hectares sampled	Basal area of the top 15 food species per hectare
DBH of <i>P. reclinata</i> class 3 and 4 stems <50% harvested	Converted to basal area, ^a added, and divided by number of hectares sampled	Basal area of <i>P. reclinata</i> per hectare
DBH of individuals (≥ 10 cm DBH) of <i>Ficus sycomorus</i>	Converted to basal area, ^a added, and divided by number of hectares sampled	Basal area of <i>F. sycomorus</i> per hectare
DBH of cut trees and <i>P. reclinata</i> class 4 stems $\geq 50%$ harvested	Converted to basal area, ^a added, and divided by number of hectares sampled	Basal area of harvested trees per hectare
DBH of <i>P. reclinata</i> class 3 and 4 stems $\geq 50%$ harvested	Converted to basal area, ^a added, and divided by number of hectares sampled	Basal area of harvested <i>P. reclinata</i> per hectare

*Unless otherwise noted, tree refers to those with a DBH of 10 cm or greater.

^aBasal area was calculated for each stem with the equation for area of a circle, $\pi(\text{DBH}/2)^2$. This was then converted from cm^2 to m^2 by dividing by 10,000.

A weighted (by the number of surveys in each forest) multiple regression analysis [Neter et al., 1985] was performed on data from the 31 fragments. I performed separate regression analyses for each subset of fragments (inside and outside the TRPNR). I also conducted analyses with the composite forest attributes. All tests were two-tailed.

RESULTS

The final sample of 31 fragments was not proportionately distributed across the eight categories ($\chi^2=19.34$; $df=7$; $P=0.072$; Table I). This disproportionate sampling resulted from problems related to location, need for security, extreme current forest clearing, or community opposition.

I sampled 107 belt transects in the 31 forest fragments (mean per fragment=3.45, SE=0.185, range=2–6). In two fragments, I was able to sample only two belt transects. In one of these fragments there was community opposition to the presence of outsiders, and in the other the fragment size was too small.

I conducted 370 mangabey surveys (mean per fragment=11.94, SE=1.623, range=1–31). In 23 fragments I did not conduct a survey for a full 12 months, for the following reasons: the month in which we started work in the fragment did not allow for a year of surveys to be conducted, the large size of the fragment made the risk of underestimating the number of groups greater than the benefit from monthly surveys, and the community's knowledge that mangabeys had been absent from the fragment for years made monthly surveys unnecessary.

There was no significant difference in the mean number of mangabey groups in fragments inside the TRPNR and those outside. Three forest attributes differed between the two subsets of fragments. The basal area of trees ≥ 10 cm DBH/ha ($z=-2.411$; $P=0.016$), basal area of harvested trees/ha ($t=-2.718$; $df=29$; $P=0.011$), and total basal area of trees ≥ 10 cm DBH/ha ($t=-3.456$; $df=29$; $P=0.002$) were significantly smaller in the fragments inside the TRPNR than in the fragments outside the TRPNR.

The mean number of mangabey groups was positively associated with fragment area and density of trees ≥ 10 cm DBH (Table IV). These variables were responsible for 75% of the variation in mangabey abundance. When only the fragments within the TRPNR were analyzed, the same variables explained 86% of the variation. Fragment area was responsible for most of the variation in the mean number of mangabey groups in both of these models. The mean number of mangabey groups outside the TRPNR was positively associated only with fragment area. However, this model explained only 42% of the variation in mangabey abundance.

An analysis incorporating the predisturbance composite variables did not improve the fit of any of the models (Table IV). The mean number of mangabey groups was positively associated with fragment area and total density of trees ≥ 10 cm DBH, consistent with the previous results. While fragment area was still significant, total density of trees ≥ 10 cm DBH was not significant within the TRPNR. Instead, total basal area of the top 15 food species was a significant variable. In both of these models, fragment area was still responsible for most of the variation in the response variable. The mean number of mangabey groups outside the TRPNR was positively associated only with fragment area, consistent with the analysis using the original variables.

TABLE IV. Final Regression Models Using Mean Number of Mangabey Groups as the Dependent Variable

Model, independent variable	Standardized coefficient	F(df) t(df)	Model R^2 partial r^2
Original variable models			
All fragments (N=31)		41.38** _(2,28)	0.75
Fragment area	0.93	9.09** ₍₂₈₎	0.67
Density of trees	0.30	2.92** ₍₂₈₎	0.08
TRPNR fragments (N=15)		36.64** _(2,12)	0.86
Fragment area	1.01	8.55** ₍₁₂₎	0.75
Density of trees	0.36	3.05** ₍₁₂₎	0.11
Non-TRPNR fragments (N=16)		10.18** _(1,14)	0.42
Fragment area	0.65	3.19** ₍₁₄₎	0.42
Composite variable models			
All fragments (N=31)		36.36** _(2,28)	0.72
Fragment area	0.89	8.53** ₍₂₈₎	0.67
Total density of trees	0.24	2.28* ₍₂₈₎	0.05
TRPNR fragments (N=15)		32.04** _(2,12)	0.84
Fragment area	0.88	7.63** ₍₁₂₎	0.75
Total basal area of top 15 food trees	0.30	2.65* ₍₁₂₎	0.09
Non-TRPNR fragments (N=16)		10.17** _(1,14)	0.42
Fragment area	0.65	3.19** ₍₁₄₎	0.42

* $P < 0.05$; ** $P < 0.01$.

DISCUSSION

Fragment area was responsible for much of the variation in mangabey abundance observed in this study. Since many of the mangabeys' top diet species have clumped distributions [Kinnaird, 1990], a larger fragment provides more individuals of these food species. A larger fragment also provides more individuals of the mangabeys' rarer diet species (many at less than two individuals per ha [Kinnaird, 1990]) and a higher number of food species [MacArthur & Wilson, 1967]. In addition, Medley [1993b] found a significant positive correlation between the number of mangabey groups and area-to-perimeter ratio, which increased as fragment size increased. The significance of the fragment area is consistent with the findings of Estrada and Coates-Estrada [1996] and Medley [1993b].

The second significant variable, density of trees, was responsible for a smaller proportion of mangabey abundance variation. Although the mangabey spends the majority of its time feeding and moving on the ground, tree density is important because the mangabeys eat food from subcanopy and canopy trees, and they require canopy trees in which to sleep. Although this variable was significant when fragments inside the TRPNR were analyzed, it was not significant for fragments outside the reserve. This lack of significance was not due to a lower "quality" of tree outside: density, basal area of the top 15 food species, basal area of *P. reclinata*, basal area of *F. sycomorus*, and mean height did not differ significantly between inside and outside. Furthermore, fragments outside actually had larger trees, as evidenced by a significantly larger basal area per ha despite the similar density.

Although the basal area of harvested trees per ha was not a significant variable in any of the models, fragments outside did have a larger measure of harvested trees. This raises the possibility that human presence and activity

alone may have a strong negative impact on mangabey abundance, masking the positive effect of total density in fragments outside the TRPNR. In several fragments, I witnessed marked changes in the mangabey groups' behavior (e.g., they moved faster, ranged farther, or left the forest) when human activity (e.g., collecting firewood, cutting poles, collecting palm wine, walking with dogs) was high.

A third variable, the basal area of the mangabeys' top 15 food species, was significant only inside the TRPNR when human forest product use was taken into account. This supports the notion of a "transient time" [Ovaskainen & Hanski, 2002] and highlights the competition between humans and mangabeys for the mangabeys' top food resources. Measures of food availability have also been found to be positively associated with primate abundance by Balcomb et al. [2000], Chapman and Chapman [1999], Mborora and Meikle [2004], Mendes Pontes [1999], and Sorensen and Fedigan [2000].

However, the basal area of food species was not a significant predictor of mangabey abundance in fragments outside the TRPNR, even though there was no significant difference in this variable inside vs. outside the reserve. The lack of significance is most likely due to our limited knowledge of the mangabeys' diet, which comes from only three fragments inside TRPNR [Homewood, 1976; Kinnaird, 1990; Wieczkowski, 2003]. Medley [1992] found that canopy tree composition within TRPNR was only 29% similar to that at the southern limit of the mangabey's distribution. Lists of diet species are likely to vary across the mangabey's distribution because of this variation in species composition, limiting the strength of the current list to measure food abundance distribution-wide. This is similar to a finding by Onderdonk and Chapman [2000], who reported that the number of food trees did not significantly explain variation in the presence or absence of three primates. In their study, diet data came from primate populations inside Kibale National Park, Uganda, while the presence/absence data were collected in forest fragments outside the park, where tree species composition and diet potentially differed.

Competitive release [Peres & Dolman, 2000; Tutin, 1999] and interspecific competition [Mitani et al., 2000] have been found or hypothesized to be the cause of observed densities of several primate species. A potential competitor of the Tana mangabey, the yellow baboon, was not investigated in the current study. The data obtained to date are equivocal. Wahungu [1998] found that Tana mangabeys spent significantly less time in a 1-ha grid if baboons were present in the same grid. This suggests that the baboons impacted mangabey foraging efficiency, which is supported by observations of frequent supplantations of mangabeys by baboons. Diet and habitat overlap indices between the two species, however, were low during the period of low fruit availability, when competition would have been most severe. Considering these findings, further investigation is warranted to determine whether yellow baboons are having a negative impact on the mangabey population.

In order to manage the Tana River forest fragments best for the mangabey, management should focus on those forest attributes that were significantly correlated with variation in mean number of groups per fragment—primarily forest area, density of trees, and basal area of the top 15 food trees (at least within the TRPNR). It is clear that local authorities and TRPNR management must actively enforce the national moratorium on the cutting of indigenous forest, especially within the Tana River Primate National Reserve, and find a permanent solution for the problem of people clearing forest for farmland within the TRPNR. Forest restoration activities can enlarge forest fragments, provide additional food

resources, and connect isolated fragments. Restoration activities that were recommended and/or initiated in the past [Medley, 1994; World Bank, 1996] should also be completed. Although some level of human activity is allowed within national reserves [Government of Kenya, 1976, 1989], it must be well managed, especially human use of mangabey diet species. Less damaging alternatives to current forest product use do exist [Mbora & Wieczkowski, 2001], and their use should be encouraged. Beyond this, research should be expanded to study the diet of groups living in other areas of the 60-km distribution, especially in the south where species composition of the fragments differs [Medley, 1992]. This would provide spatially-specific lists of important diet species. This information will greatly contribute to management planning for both forest restoration and restriction of human forest product use.

ACKNOWLEDGMENTS

I thank the Government of Kenya for permitting this research (permit OP/13/001/27C 90), and Kenya Wildlife Service for the research affiliation. I acknowledge Dr. David Mbora for allowing me to use the vegetation sampling methods he proposed, and collaborating in the data collection. Dr. Jaxk Reeves and Ms. Yan Jiang of the Statistical Consulting Center at the University of Georgia provided help with the analyses. Special thanks go to Drs. Carolyn Ehardt and David Mbora for valuable comments and suggestions. Dr. Irwin Bernstein and three anonymous reviewers provided further editorial assistance. Dr. Margaret Kinnaird provided access to unpublished data. Finally, this work would not have been possible without the support of the people of Tana, especially our field assistants (Abio Gafo, Hassan Jillo, Michael Moroa, John Kokani, Galana Galole, Galana Jumaa, Komora Phanuel, and Zakaria Maro).

REFERENCES

- Andrews P, Groves CP, Horne JFM. 1975. Ecology of the lower Tana River flood plain (Kenya). *JE Afr NH Soc Nat Mus* 151:1–31.
- Balcomb SR, Chapman CA, Wrangham RW. 2000. Relationship between chimpanzee (*Pan troglodytes*) density and large, fleshy-fruit tree density: conservation implications. *Am J Primatol* 51:197–203.
- Brower JE, Zar JH, von Ende CN. 1998. Field and laboratory methods for general ecology. Boston: WCB McGraw-Hill. 288 p.
- Butynski TM, Mwangi G. 1994. Conservation status and distribution of the Tana River red colobus and crested mangabey. Unpublished report for Zoo Atlanta, Kenya Wildlife Service, National Museums of Kenya, Institute of Primate Research, and East African Wildlife Society.
- Butynski T, Primate Specialist Group. 2000. *Cercocebus galeritus* ssp. *galeritus*. In: IUCN 2003. 2003 IUCN red list of threatened species. www.redlist.org. Downloaded on 17 February 2004.
- Chapman CA, Chapman LJ. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40:215–231.
- Decker BS. 1989. Effects of habitat disturbance on the behavioral ecology and demographics of the Tana River red colobus (*Colobus badius rufomitratu*s). Ph.D. dissertation, Emory University, Atlanta, Georgia. 330 p. Available from University Microfilms, Ann Arbor, MI; 9015645.
- Estrada A, Coates-Estrada R. 1996. Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *Int J Primatol* 17:759–783.
- Government of Kenya. 1976. The Wildlife (Conservation and Management) Act, 1976. Nairobi: Kenya Gazette Supplement.
- Government of Kenya. 1989. The Wildlife (Conservation and Management) Act, 1989. Nairobi: Kenya Gazette Supplement.
- Homewood KM. 1976. Ecology and behaviour of the Tana mangabey (*Cercocebus galeritus galeritus*) [dissertation]. London: University College, London.
- Hughes FMR. 1988. The ecology of African floodplain forests in semi-arid and arid zones: a review. *J Biogeogr* 15:127–140.

- Hughes FMR. 1990. The influence of flooding regimes on forest distribution and composition in the Tana River floodplain, Kenya. *J Appl Ecol* 27:475–491.
- Kahumbu P. 1992. The sustainability of fig tree (*Ficus sycomorus*) harvesting for canoes in a Kenyan reserve. Master's thesis, University of Florida, Gainesville, Florida.
- Kahumbu P, Davies G. 1993. Tana River Primate National Reserve: primate census, March 1993. *EANHHS Bull* 22:35–44.
- Kinnaird MF. 1990. Behavioral and demographic responses to habitat change by the Tana River crested mangabey (*Cercocebus galeritus galeritus*). Ph.D. dissertation, University of Florida, Gainesville, Florida. 301 p. Available from University Microfilms, Ann Arbor, MI; 9121618.
- Kinnaird MF. 1992. Competition for a forest palm: use of *Phoenix reclinata* by human and nonhuman primates. *Conserv Biol* 6:101–107.
- Lomolino MV, James HB, David R. 1989. Island biogeography of montane forest mammals in the American southwest. *Ecology* 70:180–194.
- MacArthur RH, Wilson EO. 1967. Theory of island biogeography. Princeton: Princeton University Press. 203 p.
- Marsh C. 1986. A resurvey of Tana River primates and their habitat. *Primate Conserv* 7:72–81.
- Mbora DNM, Wiczkowski J. 2001. Impacts of micro- and small enterprises on the environmental conservation of fragile ecosystems: a case study of the Tana River Primate National Reserve. In: Manzolillo Nightingale DL, editor. Micro and small enterprises and natural resource use. Nairobi: Micro-Enterprises Support Programme. p 147–161.
- Mbora DNM. 2003. Effects of forest quality and fragmentation on the distribution and abundance of the Tana River red colobus (*Procolobus rufomitratus*) in Tana River, Kenya. Ph.D. dissertation, Miami University, Oxford, Ohio. 145 p. Available from University Microfilms, Ann Arbor, MI; 3089890.
- Mbora DNM, Meikle DB. 2004. Forest fragmentation and the distribution, abundance and conservation of the Tana River red colobus (*Procolobus rufomitratus*). *Biol Conserv* 118:67–77.
- Medley KE. 1992. Patterns of forest diversity along the Tana River, Kenya. *J Trop Ecol* 8:353–371.
- Medley KE. 1993a. Extractive forest resources of the Tana River National Primate Reserve, Kenya. *Econ Bot* 47:171–183.
- Medley KE. 1993b. Primate conservation along the Tana River, Kenya: an examination of the forest habitat. *Conserv Biol* 7:109–121.
- Medley KE. 1994. Identifying a strategy for forest restoration in the Tana River National Primate Reserve, Kenya. In: Baldwin Jr AD, De Luce J, Pletsch C, editors. Beyond preservation: restoring and inventing landscapes. Minneapolis: University of Minnesota. p 154–167.
- Mendes Pontes AR. 1999. Environmental determinants of primate abundance in Maraca Island, Roraima, Brazilian Amazonia. *J Zool* 247:189–199.
- Mitani JC, Struhsaker TT, Lwanga JS. 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.
- Mittermeier RA, Konstant WR. 2002. The world's top 25 most endangered primates. Washington, DC: Conservation International.
- National Research Council. 1981. Techniques for the study of primate population ecology. Washington, DC: National Academy of the Sciences Press. 233 p.
- Neter J, Wasserman W, Kutner MH. 1985. Applied linear statistical models: regression, analysis of variance, and experimental designs. Homewood, IL: Richard D. Irwin, Inc. 1127 p.
- Njue A. 1992. The Tana River floodplain forest, Kenya: hydrologic and edaphic factors as determinants of vegetation structure and function. Ph.D. dissertation, University of California–Davis, Davis, CA. 313 p. Available from: University Microfilms, Ann Arbor, MI; 9302618.
- Onderdonk DA, Chapman CA. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *Int J Primatol* 21:587–611.
- Ovaskainen O, Hanski I. 2002. Transient dynamics in metapopulation response to perturbation. *Theor Popul Biol* 61:285–295.
- Peres CA, Dolman PM. 2000. Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* 122:175–189.
- Ross C, Srivastava A. 1994. Factors influencing the population density of the Hanuman langur (*Presbytis entellus*) in Sariska Tiger Reserve. *Primates* 35:361–367.
- Skorupa JP. 1986. Responses of rainforest primates to selective logging in Kibale Forest, Uganda: a summary report. In: Benirschke K, editor. Primates: the road to self-sustaining populations. New York: Springer-Verlag. p 57–70.
- Sorensen TC, Fedigan LM. 2000. Distribution of three monkey species along a gradient of

- regenerating tropical dry forest. *Biol Conserv* 92:227–240.
- Stevenson PR. 2001. The relationship between fruit production and primate abundance in Neotropical communities. *Biol J Linnean Soc* 72:161–178.
- Tutin CEG. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lope Reserve, Gabon. *Primates* 40:249–265.
- Wahungu GM. 1998. Diet and habitat overlap in two sympatric primate species, the Tana crested mangabey *Cercocebus galeritus* and yellow baboon *Papio cynocephalus*. *Afr J Ecol* 36:159–173.
- Wieczkowski J, Mbora DNM. 2000. Increasing threats to the conservation of endemic endangered primates and forests of the lower Tana River, Kenya. *African Primates* 4:32–40.
- Wieczkowski J. 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, Georgia.
- World Bank. 1996. The Republic of Kenya: Tana River Primate National Reserve. Project document. Washington, DC: The World Bank.
- Zar JH. 1984. *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice Hall. 718 p.