AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 140:562–571 (2009)

Links Between Habitat Degradation, and Social Group Size, Ranging, Fecundity, and Parasite Prevalence in the Tana River Mangabey (*Cercocebus galeritus*)

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KEY WORDS endangered species; habitat fragmentation; habitat loss; Kenya; primates

ABSTRACT We investigated the effects of anthropogenic habitat degradation on group size, ranging, fecundity, and parasite dynamics in four groups of the Tana River mangabey (*Cercocebus galeritus*). Two groups occupied a forest disturbed by human activities, while the other two occupied a forest with no human disturbance. We predicted that the groups in the disturbed forest would be smaller, travel longer distances daily, and have larger home ranges due to low food tree abundance. Consequently, these groups would have lower fecundity and higher parasite prevalence and richness (number of parasite species). We measured the abundance of food trees and anthropogenic activity in the forests, the groups' daily travel distances and home range sizes, and censused social groups over 12 months. We also analyzed fecal samples for gastrointestinal parasites from three of the groups. The disturbed forest had a lower abundance of food trees, and groups in this forest traveled longer distances, had larger home range sizes, were smaller, and had lower fecundity. The groups in the disturbed forest had higher, although not statistically significant, parasite prevalence and richness. This study contributes to a better understanding of how anthropogenic habitat change influences fecundity and parasite infections in primates. Our results also emphasize the strong influence of habitat quality in determining daily travel distance and home range size in primates. Am J Phys Anthropol 140:562–571, 2009.

Habitat fragmentation and loss are the main threat to biodiversity. In fact, as many as 29% of all primate species are critically threatened by fragmentation and loss of their forest habitat (Mace and Balmford, 2000; IUCN, 2008; Mittermeier et al., 2007). Thus, it is important to understand the multiplicity of effects that these habitat changes have on primates in order to design appropriate conservation measures. Because primates are highly social animals, changes in group sizes and group ranging patterns constitute important behavioral adjustments to habitat change. For any primate, the optimal group size is a compromise between the need to aggregate for protection from predators and the need to keep groups small to reduce intragroup feeding competition (Terborgh, 1983; van Schaik and van Hooff, 1983; Terborgh and Janson, 1986).

One factor that influences intragroup feeding competition is the abundance and distribution of food resources; competition is most intense when food abundance is low and food distribution is clumped (Altmann, 1974; van Schaik and van Hooff, 1983; Chapman et al., 1995). Among frugivorous primates, when food abundance decreases due to habitat changes, intragroup feeding competition should increase resulting in a decrease in group size (Clutton-Brock, 1974; Terborgh, 1983; van Schaik and van Hooff, 1983) and an increase in travel distance and range size (Isbell, 1991; Janson and Goldsmith, 1995; Onderdonk and Chapman, 2000). Furthermore, habitat loss and fragmentation should lead to decreased fecundity of social groups because birth and recruitment rates are positively correlated with habitat quality (Struhsaker, 1976; Hamilton, 1985; Gould et al., 1999; Struhsaker et al., 2004).

When social groups in degraded habitat spend a disproportionate amount of time each day foraging to satisfy their food requirements, individuals within such groups could incur other added costs (Terborgh and Janson, 1986). In particular, animals in degraded habitat should be prone to an increase in the prevalence and richness of directly transmitted parasites. Notably, foraging space and travel routes are limited within habitat fragments. Thus unlike in continuous habitat where social groups can travel longer distances to occupy separate areas and avoid fecal contamination of the environment (e.g. Freeland, 1980), animals in habitat fragments have to reuse the same habitat space intensively. This

Grant sponsors: Dartmouth College, National Geographic Society, Rufford Small Grants Foundation (to D.N.M.M.), Margot Marsh Biodiversity Foundation (to D.N.M.M. and J.W.), Wildlife Conservation Society, Conservation International's Primate Action Fund, Primate Conservation, Inc. and University of West Georgia Sponsored Operations Faculty Research Enhancement Award (to J.W.).

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Received 22 November 2008; accepted 7 May 2009

DOI 10.1002/ajpa.21113
Published online 19 June 2009 in Wiley InterScience (www.interscience.wiley.com).

repeated use of the same space increases the levels of contamination of the environment with infective stages of parasites such as eggs and larvae. Thus, intensive use of the same space influences positively the probability that parasite transmission stages such as eggs or larvae contact a host (Anderson and May, 1978, 1979; Morand and Poulin, 1998; Poulin, 1998; Packer et al., 1999), and parasite species that require high rates of transmission to persist in populations may exist only in populations with high rates of transmission (Anderson and May, 1979; Arneberg, 2002). For example, Stoner (1996) found that a troop of howler monkeys (*Alouatta palliata*) that lived in a forest fragment and used the same foraging space and routes repeatedly had significantly higher parasite intensities than a group that lived in continuous forest and rarely used the same foraging space and routes.

Furthermore, forest fragments contain more edge habitat for a given amount of core habitat (Fahrig, 2003). The increased edge effects in combination with elevated rates of transmission in habitat fragments should promote cross-species transfer and acquisition of novel parasites. For example, limited foraging space inside habitat fragments could push animals that are not strict habitat specialists to spend more time in the matrix exposing them to infection by atypical pathogens from humans and domestic animals. Thus, it has been found that the Tana River mangabey, a putative habitat generalist, has higher parasite prevalence and richness than the forest-dependent Tana River colobus (Mbora and Munene, 2006; Mbora and McPeek, 2009), and that among red colobus monkeys in western Uganda, groups in fragmented forests had higher parasite prevalence than groups found in continuous forest (Gillespie and Chapman, 2008).

In this study, we tested the hypothesis that forest habitat degradation due to human activities leads to reduced food tree abundance, which leads to smaller social groups that travel longer distances daily and have larger home ranges. Consequently, such groups would have lower fecundity and higher parasite prevalence and richness (number of parasite species per host). We tested this hypothesis with four groups of the Tana River mangabey (*Cercocebus galeritus*), found in eastern Kenya. This mangabey is a habitat generalist that is mostly terrestrial and ranges widely in disturbed and undisturbed habitat (Homewood, 1976, 1978; Kinnaird, 1990; Wieczkowski and Butynski, in press).

Two of our study groups lived in a forest fragment that we designated, a priori, to have high levels of anthropogenic forest degradation (referred to as "disturbed" hereafter) based on our earlier work in that forest (Wieczkowski and Mbora, 2000). The anthropogenic activities included the cutting of canopy trees to build canoes, cutting of subcanopy trees for building poles, destructive tapping of palm wine from the palm *Phoenix reclinata*, and the clearance of forest for farmland. The other two groups lived in a forest fragment with no anthropogenic activity (referred to as "undisturbed" hereafter; Wieczkowski and Mbora, 2000). The local communities do not hunt monkeys and none of our study groups engaged in crop raiding.

We predicted that the disturbed forest would have a low abundance of mangabey food trees because use of forest trees by humans and mangabeys overlaps extensively in the Tana River (Homewood, 1978; Kahumbu, 1992; Kinnaird, 1992; Medley, 1993a). We also predicted smaller social groups with lower fecundity in the forest with low mangabey food tree abundance (Medley, 1993b); these groups would travel longer distances each day and therefore would have larger home ranges. As the forest with low food, tree abundance may also have areas of minimal value to the mangabeys (e.g. cleared, previously forested areas), we predicted that those groups would have greater variation in their half-hour distances as animals would travel quickly through nonforest areas and travel more slowly (i.e., short distances) through forested areas. Finally, we expected mangabeys in the forest with low food tree abundance to exhibit a higher prevalence and richness of gastrointestinal parasites because such groups would travel more each day and were likely to reuse foraging space more often and thus increase their probability of acquiring infections. We focused on gastrointestinal parasites because the species commonly found in the Tana River mangabey are directly transmitted and are relatively easy to sample from feces (Mbora and Munene, 2006).

MATERIALS AND METHODS

Study area and species

The Tana River forest ecosystem comprises approximately 26 km^2 of gallery forest patches in the floodplain of the Tana River in eastern Kenya [1° 40′–2° 15′ South, 40° 05′–40° 10′ East; (Mbora and Meikle, 2004)]. The Tana River mangabey is endemic to these gallery forests. Due to its limited distribution and the severe loss and fragmentation of its habitat (Wieczkowski and Mbora, 2000), the Tana River mangabey is listed as Endangered (IUCN, 2008). Forest degradation and loss are caused by a growing human population that is increasingly dependent on resources extracted from the forest and on clearing land for cultivation. The area receives a mean annual precipitation of less than 500 mm mostly limited to March–June and November–December, and has mean daytime temperatures ranging from 30 to 38°C (Hughes, 1988). Thus, the gallery forest is primarily dependent on the river flooding and the height of the groundwater table (Hughes, 1988).

The diet of the Tana River mangabey comprises mainly seeds (annual mean = 42%) and fruit at all stages of development (annual mean = 32%; Homewood, 1976; Kinnaird, 1990; Wieczkowski, 2003; Wieczkowski and Butynski, in press). Although researchers have recorded 101 plant species (including 32 trees and four lianas) as contributing to the diet of the Tana mangabey, eight tree species individually account for >10% of the annual diet (Homewood, 1976; Kinnaird, 1990; Beentje, 1994; Wieczkowski J, unpublished data).

This study was conducted in two forest patches, the Mchelelo West complex and Wenje East. The Mchelelo West complex (Guru South forest, Mchelelo Research Camp, and Mchelelo West forest) has a total area of 54 hectares (see Fig. 1), while the Wenje East forest has an area of 408 hectares (see Fig. 2). However, Wenje East forest is highly disturbed by anthropogenic activities (Wieczkowski and Mbora, 2000). The local people engage in a form of shifting cultivation where they clear an area of one acre or less, grow crops and abandon the field when fertility is depleted. Such abandoned areas are prevalent in the Wenje East forest and we refer to them as "non-forest" hereafter.

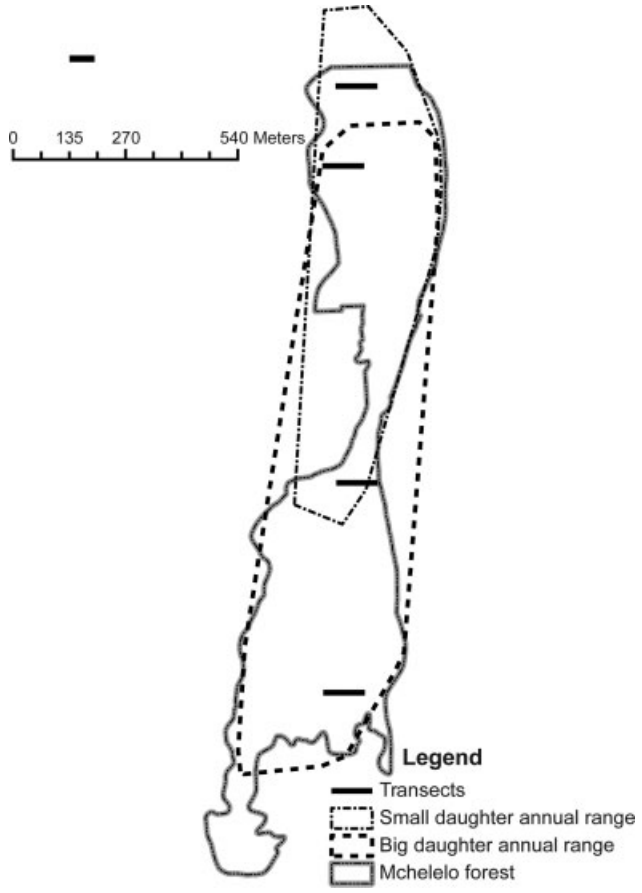

Fig. 1. The Mchelelo West forest complex showing the annual home ranges of Big Daughter and Small Daughter groups.

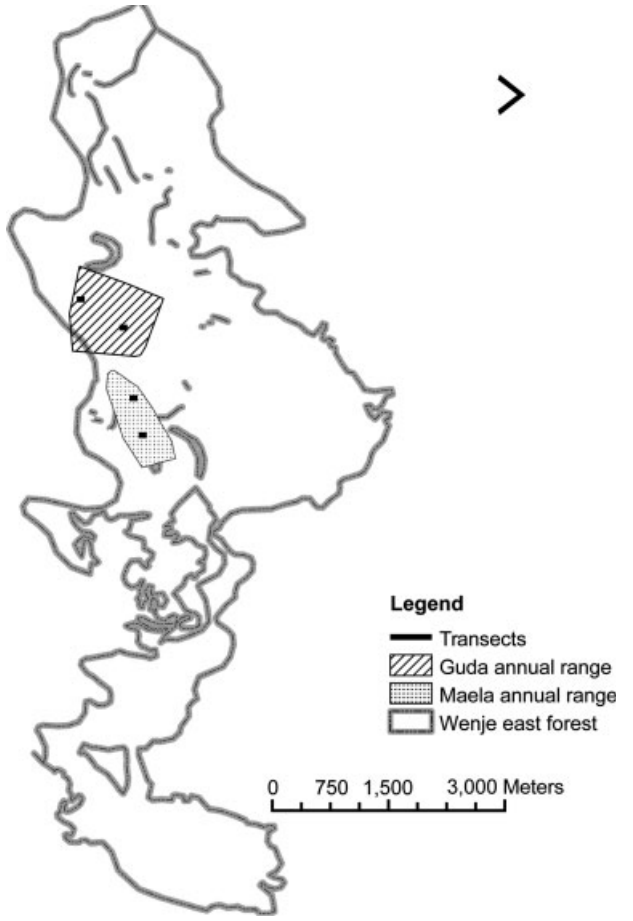

Fig. 2. Wenje East forest showing the annual home ranges of the Maela and Guda groups.

Abundance of food trees and of *Phoenix reclinata* and level of anthropogenic activity

We collected habitat data in the home ranges of the four mangabey groups by systematically establishing belt transects that were 5 m wide and 100 m long and perpendicular to the river channel within each forest (Mbora and Meikle, 2004; Wieczkowski, 2004). In each transect, we identified the species and measured diameter at breast height (DBH) of each tree $\geq$10 cm DBH. We analyzed data from two transects found within the home ranges of each of the social groups (Figs. 1 and 2). However, because the home ranges of the two Mchelelo West groups overlapped, they shared two transects. Thus, effectively, we sampled three transects for each group in Mchelelo forest (see Fig. 1). We measured the DBH of trees because DBH is an accurate estimate of fruit biomass in tropical forest trees (McDiarmid et al., 1977; Chapman et al., 1992).

We generated a list of the mangabey's top 15 diet species by analyzing the annual diets of six mangabey groups (Homewood, 1976; Kinnaird, 1990; Wieczkowski J, unpublished data). We calculated average percent contribution (to total feeding records) of each plant species, and noted the top 15. These 15 species contributed an average of 82.3% to the plant diet of eight mangabey groups (range 69% – 93.4%; Homewood, 1978; Kinnaird, 1990; Wieczkowski J, unpublished data). One of the 15 diet species is *P. reclinata*, a palm common in the Tana forests. It accounts for almost a quarter of the mangabey's annual plant diet (mean 24.1%), is eaten in every month, accounts for up to 71% of its monthly diet at times, was the number one plant species eaten in 41% of months, and was in the top five plant species eaten in 82% of months (Homewood, 1976; Kinnaird, 1990; Wieczkowski J, unpublished data). As such, we investigated its abundance separately from the other diet species. This palm can be classified into four size classes (Kinnaird, 1992). Because we were interested in measuring food availability, we recorded individuals in the reproductive classes, Class 3 (obvious trunk <2 m tall) and Class 4 (obvious trunk $\geq$2 m tall). Furthermore, because complete or near-complete removal of fronds and/or cutting of the stem affect reproductive potential in *P. reclinata* (Kinnaird, 1992), we included only individuals that had suffered less than 50% removal of fronds or no cutting of the stem in the estimation of available *P. reclinata*. *P. reclinata* grows in tight clusters and thus we could not measure the DBH of every stem. We therefore used an average (calculated from a sample of measured individuals) of 15.3 cm DBH as an estimate for basal area. Three other diet species, *Oncoba spinosa*, *Polysphaeria multiflora*, and *Saba comorensis*, begin to reproduce at DBHs <10 cm; we therefore recorded individuals of these species that were less than 10 cm but that showed signs of reproductive activity (flowers, fruits, or their remains). For these individuals, we used

an average (calculated from a sample of measured individuals) of 8 cm DBH when calculating basal area.

In order to quantify the levels of anthropogenic activity within the transects, we identified species of cut stems and measured their diameter at the cut. In addition, *P. reclinata* 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.

We calculated basal area per stem with the equation for area of a circle, π (DBH/2)^2 in square meters. We divided the basal areas of stems of dioecious species by two. We calculated a basal area per hectare of the top 15 diet species in each group's home range by dividing the basal area of all stems of those species by the area sampled in the transect (0.1 hectares). We also calculated the basal area per hectare of *P. reclinata* in each group's home range. We calculated the basal area per hectare of harvested stems and of harvested *P. reclinata* in each group's home range. In addition, we compared the mean basal area per stem of all trees $\geq$10 cm DBH among the four home ranges. The basal area data were not normally distributed so we used a Kruskal-Wallis test to check for an overall difference among the four groups, and applied Mann-Whitney tests for pair-wise comparisons (Zar, 1999).

Mangabey group variation in half-hour distances, group daily travel distance, and home range

We collected ranging data for two habituated groups of mangabeys in Wenje East from September 2005 to August 2006 and two habituated groups in Mchelelo West from July 2005 to June 2006. Therefore, our data cover both the dry and wet seasons. We collected ranging data on the two Wenje East groups (identified as Guda and Maela) over 6 days every month from 07:00 to 18:15 hours. On the first 2 days, we followed the groups without recording any data except for censusing of group age-sex composition. Every half-hour, for the subsequent 4 days, we estimated the group's center of mass by sight and recorded it using a Garmin GPS 12XL receiver. We then input the half-hour coordinates into MapSource, a trip and waypoint manager computer software (Garmin, Version 6.0). Due to the longer-term study of the Mchelelo West mangabey groups and the need to maintain consistency in methodology for those groups (Wieczkowski, 2005), we used a different but ultimately comparable method to collect ranging data for the Mchelelo West groups (identified as Big Daughter and Small Daughter). We followed the groups from 07:00 to 18:15 hrs for four days every month. Every half-hour, we spent 5 minutes marking the location of each individual on scaled maps drawn of the study area. We determined the group's center of mass as the center of a polygon drawn around all sighted individuals for each sample (Waser and Floody, 1974). For all groups, we measured half-hour distance as the distance traveled between consecutive samples, and measured it by MapSource for the Wenje East groups and with a ruler for the Mchelelo West groups.

We calculated a coefficient of variation (CV) of the half-hour distance for each group. The CV is a more ecologically interpretable measurement of variation than the standard deviation (SD) because it uses the mean in addition to the SD; the CV is calculated as the standard deviation of the half hour distances divided by the mean (Gotelli and Ellison, 2004). We added the half-hour distances to calculate a daily distance traveled each day for each group. As the data were not normally distributed, we used a two-tailed Friedman test to determine if there was a difference in mean (of 48 days); daily distances traveled among the groups, with two-tailed post hoc Wilcoxon Signed Ranks tests to check for pair-wise differences (Zar, 1999).

We calculated daily and monthly home range sizes using the minimum convex polygon method (Hayne, 1949). To make the calculations comparable between the two data collection methods, we used only the center of mass markings for the Mchelelo groups to measure home range size. For the Wenje groups, we used MapSource to estimate home range size. For the Mchelelo groups, we estimated home range size with ArcViewGIS 3.3. Both of these programs return the area of a polygon drawn around the outside locations. Because the data were not normally distributed, we used a two-tailed Friedman test to determine if there was a difference in mean (of 48 days) daily range size and a difference in mean (of 12 months) monthly range size among the groups, with two-tailed post hoc Wilcoxon Signed Ranks tests to check for pair-wise differences (Zar, 1999).

Group sizes and reproductive performance (fecundity)

We collected age-sex composition and group size data from each of the study groups as often as possible during the all-day follows. Age–sex categories follow those defined by Homewood (1976). Following Treves (2001), we defined group reproductive performance as the observed number of immatures (infants and juveniles) minus the expected number of immatures in the group. We calculated the expected number of immatures as the population mean of immatures per adult female multiplied by the number of adult females in each group. We calculated the population mean of immatures per adult female by dividing the total number of immatures by the total number of adult females (n = 15; this study; Kinnaird and O'Brien, 1991; Wieczkowski J, unpublished data). Reproductive performance is calculated based on the assumption that all immatures observed in a group were born in that group. We are confident that using both infants and immatures in the calculation of reproductive performance does not negate this assumption; male infants and juveniles do not transfer between groups and females are philopatric in this species (Homewood, 1976). Thus, the number of immatures observed in the group is a good indicator of recent birth rate, and survival of infants and juveniles. The variance in group size between counts could be due to counting error, birth, or deaths. Because the counts of the same groups at different points in time were not independent, we used a Kruskal-Wallis test to check for an overall difference among the four groups, and applied Mann-Whitney tests for pair-wise comparisons (Zar, 1999).

Parasite prevalence and richness

We collected fecal samples from the two Wenje East forest groups, and from the Big Daughter group in Mchelelo forest in July and August of 2005 and of 2006, by following them from 06:00 hour to 11:30 hours, and then from 15:00 hours until nightfall. Upon observing an animal defecating, we collected a sample of the feces and stored it in a 20-ml vial containing 10% formalin as a preservative. We labeled the vial with the date, and a code identifying the troop, age, sex, and identity of the monkey. We aimed to sample as many individuals from each social group as pos-

TABLE 1. Food tree abundance, demographic data and ranging for four groups of the Tana River mangabey in Kenya

	Mchelelo West forest (undisturbed)		Wenje East forest (disturbed)	
Measure/group	Big Daughter	Small Daughter	Guda	Maela
Basal area of top 15 food trees (m^2/ha)	22.1	35.0	15.4	7.7
Basal area per stem of top 15 food trees (m^2) ± SE[a]	0.034 ± 0.005 (*0.009*)	0.052 ± 0.015 (*0.009*)	0.021 ± 0.005 (*0.005*)	0.014 ± 0.004 (*0.005*)
Basal area of *P. reclinata* (m^2/ha)	1.8	2.7	0	0
Basal area of harvested stems (m^2/ha)	0	0	2.2	0.5
Basal area of harvested *P. reclinata* (m^2/ha)	0	0	1.7	0
Mean group size ± SE (n = 6)[a]	40.3 ± 2.7 (*41.5*)	25.8 ± 1.7 (*27*)	32 ± 0.5 (*32*)	30.5 ± 0.4 (*30.5*)
Mean reproductive performance ± SE (n = 6)[a]	1.1 ± 2.0 (*1.5*)	−1.8 ± 0.9 (*−2.2*)	−7.5 ± 1.0 (*−7.2*)	−5.5 ± 0.4 (*−5.4*)
CV of half-hour distance (%)	64.0	57.1	93.5	96.1
Mean daily travel distance (m) ± SE (n = 48)[a] (range of values)	1,408 ± 67 (*1,242.0*) (737–2,858)	1,505 ± 63 (*1,449.5*) (722–2,856)	2,456 ± 128 (*2,382.5*) (757–5,061)	2,618 ± 129 (*2,503.5*) (1,074–5,167)
Mean daily range (ha) ± SE (n = 48)[a] (range of values)	9.1 ± 0.64 (*8.0*) (2.8–23.4)	8.3 ± 0.48 (*8.6*) (2.9–14.7)	13.5 ± 1.2 (*12.4*) (2.4–31.3)	8.8 ± 0.75 (*7.0*) (2.3–27.1)
Mean monthly range (ha) ± SE (n = 12)[a] (range of values)	22.6 ± 1.8 (*22.5*) (12.7–32.5)	17.5 ± 0.73 (*17.6*) (15–23.8)	34.8 ± 4.0 (*35.1*) (16.3–62.8)	19.6 ± 3.0 (*15.9*) (6.4–45.4)
Annual home range (ha)	50.9	29.7	101	57.2
Prevalence of parasites[a] (proportion)	0.79	–	95	88
Parasite richness (number of species per host[a])	2.25 ± 0.2 (n = 36)	–	2.63 ± 0.15 (n = 55)	2.56 ± 0.18 (n = 48)

The median values are in italics. Note that most of the statistical tests remain significant after a Bonferroni adjustment (α = 0.01).
[a] See text for results of statistical tests, df = 2.

sible. We then examined the samples for gastrointestinal parasites at the Institute of Primate Research in Nairobi, Kenya, in August and September of 2005 and of 2006. We used a modified formalin-ether-sedimentation method to diagnose the presence of ova, cysts, and larval parasite stages in stool samples (Long et al., 1985). The detailed procedure used to diagnose and identify parasites is described in Ash and Orihel (1991) and the specific modifications are outlined in Mbora and Munene (2006). We measured parasite prevalence as the proportion of infected hosts in each social group (Margolis et al., 1982), and richness as the number of different parasite species detected in each host. We further classified the parasites as known pathogenic species or known non-pathogenic species, calculated the prevalence and richness of each class, and compared the prevalence and richness between the three groups. Finally, we compared the prevalence, among the three groups, of the top four most prevalent pathogenic parasites. The data on parasite prevalence and richness were normally distributed, so we used a two-tailed one-way ANOVA to test for differences in the prevalence and richness of parasites among the three groups, with two-tailed post hoc LSD tests to check for pairwise differences (Zar, 1999).

RESULTS

Abundance of food trees and of *Phoenix reclinata* and level of anthropogenic activity

The home range of the Small Daughter group had the largest basal area of the top 15 diet species per hectare while the Maela group had the lowest (Table 1). The home range of the Small Daughter group had a larger mean basal area per stem (n = 101) than either the group in Guda (n = 72; U = 1,933.5; $P < 0.0005$) or in Maela (n = 54; U = 1,327.0; $P < 0.0005$) (Table 1). The Big Daughter group also had a larger mean basal area per stem (n = 99) than either Guda (U = 1,979.5; $P < 0.0005$) or Maela (U = 1,344.5; $P < 0.0005$). There was no difference between Maela and Guda, but Small Daughter had a larger mean basal area per stem than Big Daughter (U = −2.209; $P < 0.027$). The Small Daughter and Big Daughter groups had access to *P. reclinata*, while no reproductive individuals of this palm species were found in the home ranges of the groups in Wenje East (Table 1).

The Guda group encountered the highest level of anthropogenic activity and the Maela group the second highest; neither Mchelelo West group encountered any anthropogenic disturbance (Table 1). The Guda group also encountered harvested *P. reclinata* in its home range (Table 1).

Group sizes and reproductive performance (fecundity)

Big Daughter was the largest group on average while Small Daughter was the smallest; Guda and Maela were intermediate in size (Table 1). Pairwise comparisons indicated that the Big Daughter group was larger than the Small Daughter group (U = 1.000; P = 0.004) and the Maela group (U = 5.500; P = 0.041), but not the Guda group. Guda was larger than the Maela group (U = 5.500; P = 0.041). Small Daughter was smaller than both Maela (U = 1.000; P = 0.004) and Guda (U = 0.000; P = 0.002).

TABLE 2. Prevalence of gastrointestinal parasites in three social groups of Tana River mangabey in Kenya

Parasites species	Prevalence − (% of samples infected)			Taxonomic group and life cycle comments (Roberts and Janovy, 2005)
	Big Daughter	Maela	Guda	
Abbreviata spp.	0.8	0.0	0.0	Nematode, indirect
Ascaris spp.	0.0	0.6	0.0	Nematode, direct, pathogenic in humans
Capillaria spp.	12.0	13.0	14.0	Nematode, direct or indirect, pathogenic in humans
Heterakis spp.	36.0	27.0	23.0	Nematode, direct, pathogenic in humans
Physaloptera spp.	0.0	0.6	0.6	Nematode, indirect, pathogenic in humans
Strongyloides spp.	0.0	0.0	0.6	Nematode, direct or indirect, pathogenic in humans
Toxascaris spp.	0.8	0.6	1.2	Nematode, direct[a], pathogenic in humans
Toxocara spp.	0.5	0.6	0.6	Nematode, direct[a], pathogenic in humans
Trichostrongylus spp.	0.8	2.9	2.9	Nematode, direct, pathogenic in humans
Trichuris spp.	0.8	1.7	3.5	Nematode, direct, pathogenic in humans
Anoplocephala spp.	0.8	0.0	0.6	Cestode, indirect, pathogenic in humans
Bertiella spp.	2.10	0.0	0.5	Cestode, indirect, benign in primates
Dicrocoelium spp.	0.0	0.0	0.58	Trematode, indirect
Balantidium coli-like[b]	16.0	29.0	43.0	Protozoa, causes balantidiasis in humans
Entamoeba coli	24.5	27.34	10.50	Protozoa, common, benign in primates
Entamoeba hartmani	10.0	10.5	10.5	Protozoa, not pathogenic
Entamoeba histolytica-like[b]	57.0	67.0	55.0	Protozoa, causes amoebic dysentery in humans

[a] Probably orally ingested rather than being infectious.
[b] The species were identified as -like because of the uncertainty of species identification. We identified them based on the size, number, and the morphology of the nuclei in the recovered cysts. However, it is possible that *E. histolytica*, could be *Entamoeba dispar* or a distinct species. Similarly, several different ciliates, e.g. *Buxtonella,* resemble *Balantidium* spp.

Big Daughter had the highest, and only positive, mean reproductive performance value, followed by Small Daughter, Maela, and Guda (Table 1). Both Mchelelo West groups had larger values than the Wenje East groups. Big Daughter's value was larger than Maela's ($U = 0.000$; $P = 0.002$) and Guda's ($U = 0.000$; $P = 0.002$). In addition, Small Daughter's value was larger than Maela's ($U = 0.000$; $P = 0.002$) and Guda's ($U = 0.000$; $P = 0.002$). There was no difference in reproductive performance between the Mchelelo West groups or between the Wenje East groups.

Group variation in half-hour distance, group daily travel distance, and size of home range

The Wenje East groups had much larger CVs of half-hour distances than the Mchelelo West groups (Table 1). The mean daily travel distance of the Guda group was significantly longer than those of both Big Daughter ($Z = -5.262$; $P < 0.0005$) and Small Daughter ($Z = -5.128$; $P < 0.0005$) (Table I). The Maela group also traveled significantly longer on average than Big Daughter ($Z = -5.262$; $P < 0.0005$) and Small Daughter ($Z = -5.185$; $P < 0.0005$) (Table 1). There was no difference between the mean daily travel distance of Maela and of Guda, or between that of Big Daughter and of Small Daughter.

The mean daily range of the Guda group was significantly larger than that of Big Daughter ($Z = -2.741$; $P = 0.006$), Small Daughter ($Z = -3.072$; $P = 0.002$), and Maela ($Z = -3.164$; $P = 0.002$) (Table 1). The mean monthly range of the Guda group was also significantly larger than that of Big Daughter ($Z = -2.353$; $P = 0.019$), Small Daughter ($Z = -2.824$; $P = 0.005$), and Maela ($Z = -2.510$; $P = 0.012$). In addition, Big Daughter's mean monthly range was larger than that of Small Daughter ($Z = -2.275$; $P = 0.023$). There were no significant differences among the daily and monthly range sizes of Maela, Small Daughter, and Big Daughter. Guda's annual home range was the largest of the four groups, followed by Maela, Big Daughter, and Small Daughter.

Parasite prevalence and richness

We analyzed 185 fecal samples from three groups as follows: Big Daughter 54, Guda 68, and Maela 63. We found 13 helminths and four protozoans with the protozoans exhibiting the highest prevalence (Table 2). The overall prevalence of parasites was statistically different among the three groups (ANOVA, $F = 4.01$, $P < 0.02$). The prevalence of parasites was lower in Big Daughter than in Guda (0.79 vs. 0.95; SE = 0.059, $P < 0.01$). However, the differences in prevalence between Big Daughter and Maela (0.79 vs. 0.88, SE = 0.06, $P > 0.14$) and between Guda and Maela (0.95 vs. 0.88, SE = 0.057, $P > 0.17$) were not statistically significant. The prevalence of pathogenic parasites was analogous to that of the overall prevalence of parasites. The prevalence of pathogenic parasites was statistically different among the three groups (ANOVA, $F = 4.046$, $P < 0.02$). The prevalence of pathogenic parasites was lower in Big Daughter than in Guda (0.73 vs. 0.92; SE = 0.067, $P = 0.00$). However, the differences in prevalence between Big Daughter and Maela (0.73 vs. 0.83, SE = 0.067, $P > 0.16$) and between Guda and Maela (0.93 vs. 0.83, SE = 0.065, $P > 0.15$) were not statistically significant.

We detected a total of 17 parasite species in the three groups: Big Daughter 13, Guda 15, and Maela 12 (Table 2). Overall, the mean number (±SE) of parasite species per host was lower in the Big Daughter (2.25 ± 0.2) than Guda (2.63 ± 0.15) and Maela (2.56 ± 0.18) groups, but these differences were not statistically significant (ANOVA, $F = 1.22$, $P > 0.3$). Similarly, the mean richness of pathogenic parasites was higher in Guda (1.63 ± 0.109) than in Maela (1.56 ± 0.126) and Big Daughter (1.29 ± 0.134) but these differences were not statistically significant (ANOVA, $F = 2.11$, $P > 0.12$). Neither the prevalence nor the number of non-pathogenic parasites differed among the three groups (ANOVA; prevalence, $F = 0.97$, $P > 0.38$; richness, $F = 0.04$, $P > 0.97$).

The four most prevalent pathogenic parasites were *Capillaria spp., Heterakis spp., Balantidium coli*-like, *and Entamoeba histolytica*-like (Table 2). Only the prevalence

of *Balantidium coli*-like differed among the three groups (ANOVA, $F = 5.5$, $P < 0.01$). The prevalence of *Balantidium coli*-like was higher in Guda (0.43 ± 0.05) than in Maela (0.29 ± 0.06), which was higher than in Big Daughter (0.16 ± 0.06). However, only the difference between Guda and Big daughter was statistically significant (mean difference = 0.27, $P < 0.01$). Only the prevalence of the two protozoan parasites, taken together, differed among the three groups (ANOVA, $F = 6.53$, $P = 0.00$); the prevalence of the two nematodes was not different among the three groups. The prevalence of *Balantidium coli*-like and *Entamoeba histolytica*-like, taken together, was higher in Guda, than in Big daughter (mean difference = 0.27, $P = 0.00$) and in Maela (0.19, $P < 0.01$). Although the prevalence of *Balantidium coli*-like and *Entamoeba histolytica*-like, taken together, was higher in Maela than Big daughter this difference was not statistically significant (mean difference = 0.1, $P > 0.3$).

DISCUSSION

Overall, our data strongly suggest that reduced food tree abundance was associated with smaller social groups that had reduced reproductive performance, traveled longer distances daily, and had larger home ranges. These smaller groups also had higher prevalence and richness of parasites. The two groups of mangabeys in Wenje East, a forest that is highly degraded by anthropogenic activity, had access to a lower abundance of important food trees than the mangabey groups in Mchelelo West, a forest with no anthropogenic activity. In addition, the mangabey groups in Wenje East had no access to reproductive *P. reclinata*, the Tana River mangabey's most important food species. *P. reclinata* is a critical resource for the mangabeys because it fruits out of synchrony with other diet species and thus is available when other diet species are not (Kinnaird, 1992). All the *P. reclinata* that occurred in our belt transects in Guda's home range had been utilized by humans to the extent that it was no longer reproductive.

The findings outlined above are consistent with other studies of the Tana River mangabey. For example, Decker and Kinnaird (1992) found that average mangabey group size declined from 26 to 17 individuals between 1974 and 1987, likely due to forest loss and degradation. In addition, Medley, 1993b showed that the number of Tana River mangabey individuals per forest is positively correlated with *P. reclinata* density and the ratio of the area of the forest to its perimeter distance (area-to-perimeter ratio). Generally, more disturbed forests would have a lower area-to-perimeter ratio than less disturbed forests. Thus, the number of Tana River mangabeys was also negatively correlated with intraforest heterogeneity (a measure of intraforest disturbance such as tree cutting) (Medley, 1993b). Presumably, the Wenje East groups, facing an absence of *P. reclinata* and a lower abundance of other food tree species due to forest degradation, were smaller than the Big Daughter group in Mchelelo West. Reduction in group size due to habitat destruction or degradation has also been seen in red-tail monkeys (*Cercopithecus ascanius schmidti*) in forest fragments in Uganda (Baranga, 2004), a howler monkey (*Alouatta palliata*) group whose habitat was deforested in Costa Rica (Clarke et al., 2002), and black-and-white colobus (*Colobus guereza*) in forest patches in Uganda (Onderdonk and Chapman, 2000). The two groups in Wenje East, however, were not smaller than the Small Daughter as we expected. The Big Daughter and Small Daughter groups are the result of a 2004 group fission (Mbora, personnel observation.). The parent group fissioned unevenly, and it may take some time for the Small Daughter group to increase to a size that is commensurate with food tree abundance.

We had also predicted that the groups in Wenje East would have greater variation in half-hour distances, travel longer distances, and use a larger home range because of their degraded, lower quality habitat. The Wenje East groups did have significantly greater variation in half-hour distances, due to their need to travel through non-forest areas in order to reach additional forest and food resources (Table 1; Mbora, personnel observation). Wieczkowski (Wieczkowski J, unpublished data) collected vegetation and mangabey behavioral data in three nonforest areas similar to those found in Wenje and used by two other mangabey groups. The nonforest areas had very low densities of the top 15 food species, and the mangabeys moved more and did not socialize as much in the nonforest areas as they did in the forested areas.

The Wenje East groups did also have significantly longer mean daily travel distances (Table 1). This was interesting because it would be expected that because the Big Daughter group was larger, it should have traveled comparable, if not greater, distances compared with the smaller Wenje East groups. This is expected because larger groups should have increased intragroup feeding competition among frugivorous primates (Isbell, 1983; Janson and Goldsmith, 1995; Isbell et al., 1998; Wieczkowski, 2005). However, the Big Daughter group in fact traveled significantly shorter distances each day than the other two much smaller Wenje East groups (Table 1). This suggests that habitat quality (as measured by food tree abundance here) may override group size in influencing daily distances traveled. Several other studies have shown that primate groups in poorer habitats have longer daily travel distances than groups in higher quality habitats, (e.g. Barrett, 1995; Fleury and Gautier-Hion, 1999; Gillespie and Chapman, 2001; Palacios and Rodriguez, 2001; Clarke et al., 2002). For example, of the three groups of Sulawesi crested black macaques (*Macaca nigra*) studied by O'Brien and Kinnaird (1997), the smallest group had a longer daily travel distance than the middle-sized group due to its habitat containing less primary forest.

Further support for the influence of food tree abundance on group ranging comes from the comparison of the annual home range sizes. Both Wenje East groups had significantly larger ranges than both Mchelelo West groups (Table 1). In the undisturbed Mchelelo West forest, the two groups overlapped in home range, possibly sharing food resources (see Fig. 1). Despite this overlap, the Mchelelo groups still had significantly smaller home range area than the Wenje East groups (Table 1). When we compared daily and monthly range size, however, only the Guda group had larger mean daily and monthly ranges than both Mchelelo West groups.

The mean daily and monthly ranges of the Maela group were larger than those of only the Small Daughter group, while its maximum daily and monthly ranges were larger than both Mchelelo West groups. Maela ranges in a putatively low-quality habitat as measured by the basal area of the mangabey's top 15 diet species and of *P. reclinata*. Thus, it is puzzling that greater differences in daily and monthly ranging were not found between it and the Mchelelo groups. However, it must be noted that detailed studies of the diet of the Tana River mangabey have not been

conducted in Wenje East forest. Therefore, we can only speculate that perhaps the diet species and items that the Maela group is relying on are more evenly distributed or regenerate more quickly than those in the other forests regenerate allowing a smaller range.

The low and negative reproductive performances of the Wenje East groups indicated that these groups had fewer immatures than expected given the number of adult females in the group. The types of analyses we conducted do not allow us to conclude that lower food tree abundance caused this low reproductive performance. However, low habitat quality is strongly implicated because these groups also had high CVs of daily travel distances, longer daily travel distances, and larger home ranges with low amounts of food tree abundance (Table 1). Furthermore, it is well known that in social mammals where only mothers raise their young, reproductive performance either declines with increasing group size or shows no consistent relation to group size at all (e.g. Silk, 2007; van Belle and Estrada, 2008). One reason that has been advanced to explain the negative association between reproductive performance and group size is increased intragroup competition. Thus, the low reproductive performance by the Small Daughter group is puzzling given that this group had the highest abundance of food trees (Table 1). One possible reason for this low performance is a low survival rate of immatures because the group is too small to provide adequate protection from predation. Some predation attempts on mangabeys have been witnessed in Mchelelo forest (Wieczkowski, personnel observation). Alternatively, it is possible that the demographics of the Small Daughter group have not yet adjusted to its smaller size given that this group only fissioned recently, in 2004 (Mbora, personnel observation).

There was a tendency for higher parasite prevalence to be associated with longer daily travel distances and greater ranging. The social groups with the longer daily travel distances and larger ranges had higher parasite prevalence and number of parasite species, and more species requiring intermediate hosts (Table 2). However, the differences in parasite prevalence were only statistically significant between Guda and Big Daughter. Perhaps the much larger social group of the Mchelelo forest confounded the effects of habitat loss and fragmentation because larger social groups typically have a higher prevalence and richness of parasites (Freeland, 1976; Guegan and Kennedy, 1993; Loehle, 1995; Nunn and Altizer, 2006).

The total number of parasite species found in our three study groups was as many as that found in a previous survey of parasites from six mangabey groups in five forests distributed across the Tana River (Mbora and Munene, 2006). It was also equal to that found in seven species of monkeys surveyed intensively in Kibale National Park, Uganda by Gillespie et al. (2005). This high total number of parasites infecting these monkeys not withstanding, their parasite richness per host (Table 2) was quite low compared with the mean of 5.17 species per host generally found among threatened primates (Altizer et al., 2007).

Other studies in the Tana River forest (Mbora and McPeek, 2009) and in western Uganda (Gillespie and Chapman, 2006, 2008) have shown that habitat loss and fragmentation are associated with increased parasite prevalence and richness among forest primates. Several ecological mechanisms may be responsible for increased levels of parasite prevalence and richness among the mangabey groups in the disturbed forest fragment. First, the intensive use of the same foraging space may increase the rate of encounter with infective stages of parasites such as eggs or larvae and thus increase parasite prevalence in the disturbed forest (Anderson and May, 1978, 1979; Morand and Poulin, 1998; Poulin, 1998; Packer et al., 1999). In addition, parasite species that require high rates of transmission to persist would be favored in the groups within disturbed habitat, increasing their parasite richness (Anderson and May, 1979; Arneberg, 2002).

Second, the continuing habitat disturbance reduces the amounts of food resources, possibly increases competition for food among resident animals, and increases foraging costs. The combined effects of increased food competition, attendant elevated agonistic interactions among animals, and increased foraging costs could increase stress levels, compromise immunocompetence, and thereby lower resistance of animals in the disturbed forest to infection (Eley et al., 1989; Coe, 1993; Friedman and Lawrence, 2002).

Third, the increased edge effects due to habitat disturbance, combined with elevated rates of transmission, could promote cross-species transfer and acquisition of novel parasites. Animals in the disturbed forest are forced to traverse areas undergoing human activities and thus are exposed to infection by atypical pathogens from humans and domestic animals (Mbora and McPeek, 2009). Thus, it was quite interesting that most of the parasites we found are pathogenic in humans, and that they tended to have higher prevalence and richness in the groups in the disturbed forest (Table 2). Nevertheless, it would be unwise to conclude that cross-species infections were occurring between humans and mangabeys in the disturbed forest without further genetic and morphological analyses of the actual parasites. As De Gruijter et al. (2005) demonstrated in Ghana using populations of *Oesophagostomum bifurcum*, parasites that infect sympatric humans and monkeys can constitute genetically distinct populations according to host species.

Finally, four additional diurnal species of nonhuman primates are found within the Tana River forests; the Tana River red colobus (*Procolobus rufomitratus*), yellow baboon (*Papio cynocephalus cynocephalus*), Sykes' monkey (*Cercopithecus mitis albotorquatus*), and the vervet (*Chlorocebus aethiops*). Thus, interactions with these sympatric species of primates may be important sources of added infection risk among our study groups (Ezenwa, 2003). However, Tana River red colobus do not occur in the disturbed Wenje East forest, but are found in Mchelelo forest, as are the other three primate species. Therefore, if interactions among sympatric primate species were responsible for the elevated parasite prevalence and richness, the Big Daughter group should have the higher prevalence and richness.

This study contributes to basic primatology and to a fuller understanding of the effects of habitat change on primate populations. First, this is an additional case study supporting the generality that primates in degraded habitats tend to occur in smaller groups (Onderdonk and Chapman, 2000; Clarke et al., 2002; Baranga, 2004) and have longer day lengths (O'Brien and Kinnaird, 1997; Fleury and Gautier-Hion, 1999; Gillespie and Chapman, 2001; Palacios and Rodriguez, 2001; Clarke et al., 2002). Our findings indicated that groups in degraded habitats might also have correspondingly larger home ranges.

Second, we analyzed the fitness costs that may be associated with degraded habitats and found low reproductive performance and elevated parasite prevalence in smaller groups in degraded habitats. In particular, low reproductive performance is a direct fitness cost and indicates that social groups of similar size, and with similar number of adult females, could have quite different reproductive performances. Therefore, group size alone should not be used as an indicator in conservation planning of how well a population is doing in habitats under threat.

Third, our findings provide further support for behavioral flexibility of the Tana River mangabey. For example, the daily distances traveled by the Wenje East groups (regularly over 2 km and sometimes over 5 km) are unprecedented in the Tana River mangabey. The maximum measured travel distance in any group before this study was 1,900 m (Homewood, 1976). The forests in which we measured these daily travel distances are within 16 km of each other and thus highlight the great variation in behavioral strategies of this mangabey over relatively short distances. However, the very low reproductive performances observed in the Wenje East groups coupled with the relatively higher rate of parasite prevalence and richness underscores the high fitness costs incurred by primates living in degraded habitat. Thus, we recommend that analyses of reproductive performance of social groups should be considered when assessing the conservation status of primates threatened by habitat fragmentation and loss.

ACKNOWLEDGMENTS

The authors are grateful for the support of the people of Tana River, and our field assistants: Michael Moroa, John Kokani, Galana Galole, Sylvia Isaya, Rahab Hiribae, Galana Jumaa, Abio Gafo, Said Hiribae, Abeid Said, Jillo Hamisi, and the late Mohamed Moroa. The authors also thank the Government of Kenya for research permission through permits MOEST13/001/35C417/2 (DNMM) and MOEST 13/001/27C 90 (J.W.), and Kenya Wildlife Service for research affiliation. John Congleton of the Geosciences Department at the University of West Georgia provided help with ArcViewGIS. The authors thank Margaret Kinnaird, Karline Janmaat, and two anonymous reviewers for their comments, which greatly improved the manuscript. As the research presented in this manuscript was conducted on nonhuman primates in their natural habitat, we were not required to be approved by an Institutional Animal Care and Use Committee. We confirm that all research reported here adhered to the legal requirements of the Republic of Kenya.

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