ASPECTS OF THE ECOLOGICAL FLEXIBILITY OF THE TANA MANGABEY (*Cercocebus galeritus*) IN ITS FRAGMENTED HABITAT, TANA RIVER, KENYA

by

JULIE ANN WIECZKOWSKI

(Under the direction of Carolyn L. Ehardt)

ABSTRACT

This dissertation investigated the ecological flexibility of the Tana mangabey (*Cercocebus galeritus*) and its use of a fragmented habitat, within the context of its ecological flexibility. The Tana mangabey is one of the world's most endangered primates, endemic to a 60-kilometer stretch of the lower Tana River in Kenya. The strength of this study is in its examination of both the mangabey's diverse habitat and its behavior. The research had two major foci. One examined the ecological correlates of mangabey abundance, with the goal of recommending management strategies. The other extended the temporal investigation of the mangabeys' ecological flexibility by studying one mangabey group that was also studied in 1974 and in 1988-89. Thirty-one study forests were selected throughout the mangabeys' distribution. One hundred and seven vegetation belt transects were sampled and 307 mangabey surveys were conducted in these study forests. From August 2000 until July 2001, monthly 3-day samples were conducted on the mangabey group to collect behavioral, dietary, and ranging data. In addition, phenology was monitored monthly in 226 trees in 11 species across the three forests visited by that group. The Tana mangabey was found to be very general in its habitat needs; the mean number of mangabey groups per forest was positively associated with forest size, density of trees ≥ 10 cm diameter at breast height, and basal area of the top 15 food species (in forests within the Tana River Primate National Reserve). Behavioral changes exhibited by the study group can be linked to the group's increased size and diet differences. Although ecological explanations for dietary changes are limited, it was found that the mangabey does not consume ripe fruit in relation to availability. Instead, they concentrate on ripe fruit, ripe seed, unripe fruit, and/or unripe seed on a species-specific basis. Finally, the most important reason for the group's expansion of its home range was the increased group size. Overall, the research supports the conclusion that the general habitat needs and ecological flexibility of the mangabey aid their survival in their highly diverse and fragmented habitat.

INDEX WORDS: *Cercocebus galeritus*, Mangabey, Behavior, Diet, Ranging, Conservation, Primate, Forest habitat, Kenya

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DEDICATION

To my parents, Dr. Gerard Wieczkowski, Jr. and Kathleen Wieczkowski.

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CHAPTER 1

INTRODUCTION

The multifaceted project to be presented in this dissertation is an investigation of the Tana mangabey (*Cercocebus galeritus*) and its use of a fragmented habitat within the context of this highly endangered primate's ecological flexibility. The contributions to be made in understanding of this mangabey's ecological flexibility derive from examination of both its dynamic and diverse riverine forest habitat and its behavior.

The lower Tana River, Kenya, to which the mangabey is endemic, supports approximately 62 forest fragments (Fig. 1.1), which differ in size, forest structure, species assemblage, and level of human activity. Due to the meandering nature of the river, the fragments are also inconstant. The mangabey inhabits 40 of these fragments at varying abundances [Butynski & Mwangi, 1994]. Conservation International placed this species on its updated list of the 25 most endangered primates [Mittermeier & Konstant, 2002] and its already limited forest habitat (estimated at only 2,616 hectares in 1994; Butynski and Mwangi, 1994) has recently undergone extensive loss and degradation [Wieczkowski & Mbora, 1999-2000]. Considering the high structural and compositional diversity in the forest fragments along the lower Tana River, and the continual restructuring of these fragments through both natural and anthropogenic means, an initial step in the conservation of *C. galeritus* would be to obtain detailed information about its habitat needs, which may then be incorporated into management recommendations. To

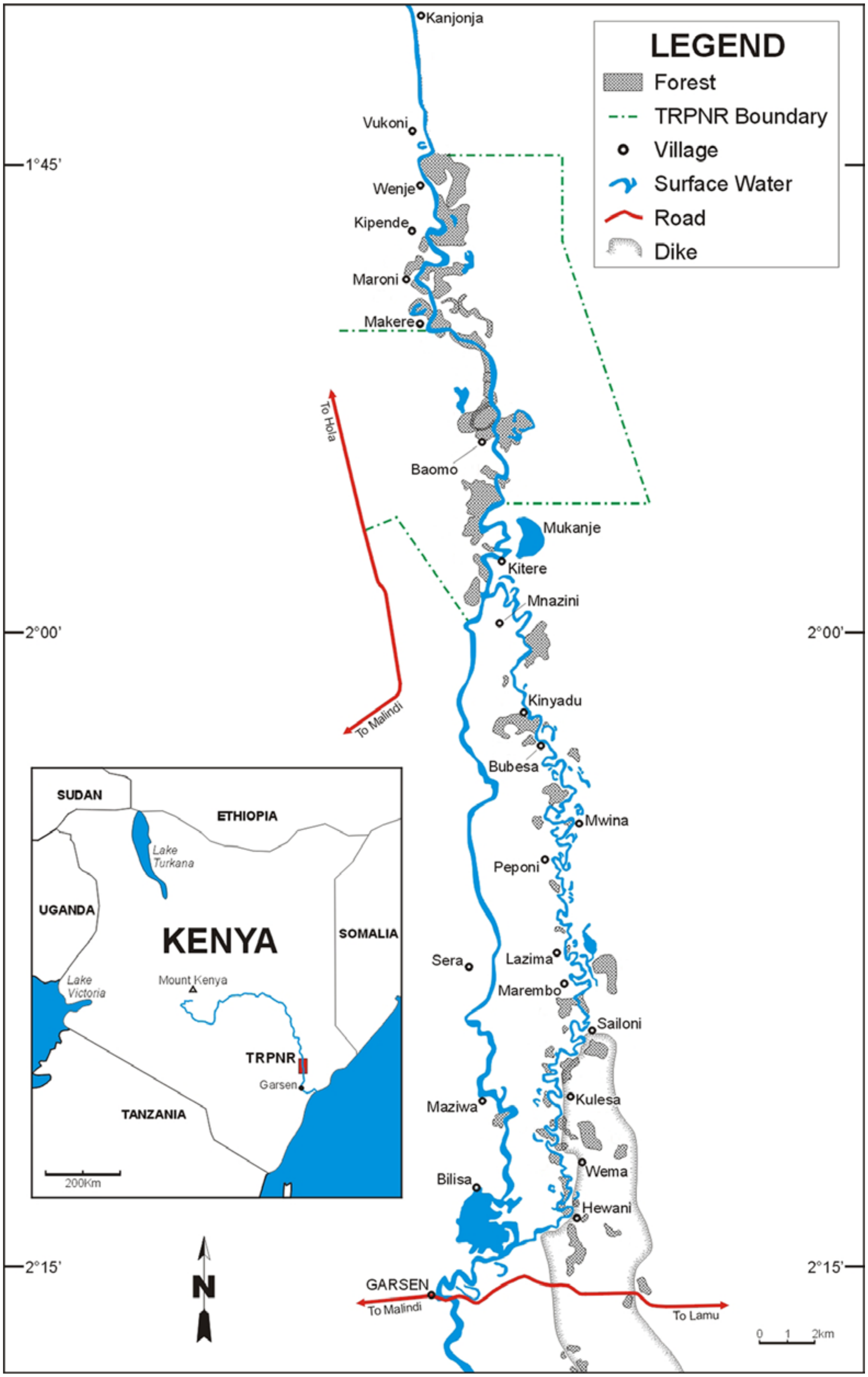

Fig. 1.1. A map of the study area, defined as the 60-kilometer distribution of the Tana mangabey (*Cercocebus galeritus*) along the lower Tana River, Kenya. Adapted from Mbora (2003).

address this question and to make a contribution to conservation and management of this critically endangered primate, I investigated the forest attributes that are most responsible for variation in mangabey abundance in 31 forests throughout the species' 60-kilometer distribution. Previous examination of the mangabey's habitat was limited to within the northwestern quarter of this diverse system; my study will therefore expand our knowledge of the mangabey's habitat to include more of the ecological diversity present within the 60-kilometer distribution.

Understanding mangabey behavior and ecology, especially that which favors the species' persistence in a fragmented environment, is also important for successful conservation. Aspects of the mangabey's ecological flexibility that have been previously investigated are temporal changes in behavior and diet. In 1988-89, Margaret Kinnaird [1990] studied two groups that had also been observed by Katherine Homewood in 1974 [1976]. Although intermittent, this long-term examination provided information about the mangabey that cannot be garnered from the study of a single group during one field season or several groups on a spatial scale. I took the opportunity to continue the study of the mangabey's ecological flexibility over a temporal scale by observing one of the groups also observed by Homewood [1976] and Kinnaird [1990], increasing the temporal dimension of the study by another 12 years. I investigated how their behavior, diet, and ranging have changed since those two earlier studies, in the context of associated ecological changes.

The forest fragments of the lower Tana River are primarily naturally created by the processes of the river and the height of the groundwater table. They are secondarily anthropogenically created, although the impact of human activity has increased in recent years. As more and more tropical forests around the world are fragmented by human activities, the intense ecological and behavioral study of the mangabey in its fragmented habitat may be able to shed light on and inform research in the growing number of such situations.

In this introduction I will provide a contextualization of the entire study within the existing literature, particularly that concerning ecological correlates of primate abundance, ecological/behavioral flexibility in primates, and primate responses to habitat fragmentation. Detailed information is provided on the lower Tana River ecosystem and the Tana mangabey, including an overview of previous research, as well as issues related to management and conservation. I will then present an overview of the general research questions that comprise each of the journal article manuscripts that constitute the "core" of the dissertation, including review of the relevant specific literature for each. Finally, a general presentation of the methods I used during the course of this study will be provided, leaving the specifics to be discussed in the respective 'chapters' (manuscripts).

Ecological Correlates of Primate Abundance

One of the most serious threats to the roughly 195 endangered and critically endangered primate taxa is habitat destruction [Mittermeier & Konstant, 2002]. As habitat degradation and destruction occur on a larger and larger scale, it becomes imperative as a first step towards conserving primates to understand the relationship between primates and their habitats. This understanding must be of both the habitat and the primate taxon. It is critical to understand both the habitat attributes that are most important in supporting primates as well as how primates respond ecologically and demographically to habitat differences. Specifically, it is important to understand how primates respond to and survive habitat fragmentation. This knowledge can then be integrated into long-term conservation plans for the primates and their habitats.

Conservation planning for a species can be made more effective if the particular habitat needs of the species in question are known. This information can be used to identify sites for protection or to guide habitat restoration activities. Such knowledge should be obtained by measuring the abundance of a species and a variety of structural and compositional habitat attributes in a variety of sites within its geographic range. These data are then examined to determine correlations between species abundance and the habitat attributes. With the exception of Biquand et al. [1992], who looked at *Papio hamadryas* distribution in Saudi Arabia, the majority of such studies to date are concerned with forest-dwelling species.

Although van Horne [1983] argues for the use of demographic variables in assessment of habitat quality, instead of the more commonly used density or abundance, only one study has examined demographic parameters in correlation with habitat parameters. Umapathy and Kumar [2000a] investigated demographic parameters of 11 groups of *Macaca silenus* in relation to habitat attributes in eight forest fragments in South India. They found that birth rate and percentage of immatures decreased with decreasing fragment area, tree density, and basal area, and that the immature/adult female ratio decreased with decreasing fragment area and basal area.

Forest area is one attribute that has commonly been correlated with primate abundance. Based on MacArthur and Wilson's [1967] species-area curve, which states that a larger area can support more species, it is generally hypothesized that a larger forest will support a greater abundance of primates. Kay et al. [1997] found more platyrrhine species in larger areas in 60 sites across South America. Similarly, area of the forest fragment was found to be correlated with the number of *Alouatta palliata* individuals in 126 forest fragments in Los Tuxtlas, Mexico [Estrada & Coates-Estrada, 1996]; *Cercopithecus mitis labiatus* presence in 199 fragments in South Africa was most affected by the area of fragment [Lawes et al., 2000]; and in Anamalai Hills, India, *Macaca silenus* and *Trachypithecus johnii* were found in proportionally more large (>50ha) than small (<50ha) forest fragments [Umapathy & Kumar, 2000b]. There are several studies, however, that did not find forest area to be an attribute predicting primate abundance. Although *Macaca silenus* and *Trachypithecus johnii* were found in more large fragments than small, area was not a predictor of presence for either species [Umapathy & Kumar, 2000b]. Fragment area also did not predict the presence of *Colobus guereza*, *Cercopithecus ascanius*, *Cercopithecus mitis*, *Procolobus pennantii*, *Pan troglodytes*, or *Lophocebus albigena* in 20 forest fragments outside Kibale National Park, Uganda [Onderdonk & Chapman, 2000].

The studies that did not find area important for primate abundance are suggesting, directly [Umapathy & Kumar, 2000b] or indirectly, that habitat quality is more important than habitat quantity. Habitat quality is often equated with food availability, which has been measured in various ways. Several studies have found primate abundance to be correlated with availability of the species' primary or keystone resource. For example, in 30 sites across the Neotropics, biomass of the large atelines (*Ateles* spp., *Brachyteles arachnoides*, and *Lagothrix lagotrica*) was positively correlated with basal area of figs, an important resource in the scarce season, and biomass of the seed predators (*Cacajao* *calvus*, *Chiropotes satanas*, and *Pithecia* spp.) was positively correlated with basal area of *Eschweilera*, their preferred diet species [Stevenson, 2001]. In Tana River, Kenya, the number of individuals per forest of another frugivore, *Cercocebus galeritus*, was positively correlated with density of *Phoenix reclinata*, their primary diet species [Medley, 1993]. Across an unlogged, a lightly logged, and a heavily logged plot in Kibale, abundance of *Cercopithecus ascanius* was positively correlated with density of *Ficus* trees [Skorupa, 1986].

Another measure of food availability that is often investigated is a small, but important, subset of diet species. Across the same three plots as surveyed for *Cercopithecus ascanius*, Skorupa [1986] found abundance of *Colobus badius* positively correlated with total basal area of trees contributing the top 80% of their annual diet. Chapman and Chapman [1999], studying the same species (but recognized as *Procolobus tephrosceles* in their study), found a positive relationship between density of the colobus and cumulative diameter at breast height of their top five food tree species, which accounted for 75% of the diet. Balcomb et al. [2000] found that chimpanzee nest density was positively correlated with density of trees that produce large, fleshy fruits, a dominant item in their diet, across six sites in Kibale.

Even when food was measured in very general terms (e.g., fruit or leaves) positive relationships have been found. Primate biomass of frugivorous species was positively correlated with fruit production in the Neotropics [Stevenson, 2001]. *Cebus capucinus* density was positively associated with food biomass, *Alouatta palliata* density with total food biomass and with leaf biomass more than with fruit biomass, and *Ateles geoffroyi* density with total food biomass and with fruit biomass more than with leaf biomass across fourteen sites in Costa Rica [Sorensen & Fedigan, 2000]. Finally, Mendes Pontes [1999] found that the most important variable explaining density and biomass differences in five cebids among forest types in Brazil was food availability, and that this relationship, not surprisingly, resulted in different forest types being of different quality to the different species. The frugivores (*Cebus olivaceus*, *C. apella*, and *Saimiri sciureus*) were more abundant in terra firme forest, which had the highest density of fruits. On the other hand, the folivores (*Ateles belzebuth* and *Alouatta seniculus*) were more abundant in mixed forest, which had fewer fruits.

Although food availability was not directly measured in certain other studies, it was hypothesized to be important because of its relationship to structural attributes that were found to influence primate abundance. Abundance of folivores has been found to be predicted by forest attributes that influence the abundance of leaves. Peres [1997] found forest heterogeneity to explain variation in *Alouatta* densities in 106 sites in Central and South America, and suggested it may be due to the high production of leaves in heterogeneous habitats. Similarly, tree density was the only predictor of *Trachypithecus johnii* occurrence because as a folivore the primate needs a variety of diet species, which would increase as density of trees increases [Umapathy & Kumar, 2000b]. Quality of the foliage is also an important correlate of folivore biomass; two indices of mature foliage quality (protein/fiber ratio and protein/(fiber and tannin) ratio) were positively correlated with colobine biomass in six sites across Africa and Asia [Oates et al., 1990]. Structural attributes that influence food availability have also been found to impact abundance of frugivores. Of three sites surveyed in Ranomafana National Park, Madagascar, *Varecia variegata*, a specialized frugivore, was not found in the most intensively logged site, presumably because logging targets trees that are important in *V. variegata*'s diet [White et al., 1995]. Umapathy and Kumar [2000b] hypothesized that canopy height was the only predictor of *Macaca silenus* presence in fragments because that species' important fruit trees are large trees.

Two studies that did not find a relationship between primate abundance and food availability are those by Onderdonk and Chapman [2000] and Furuichi et al. [2001]. In the first study, the number of food trees did not predict the presence/absence of three species in 20 forest fragments outside Kibale National Park, most likely because the choice of food trees was based on diet data from primate populations inside the park, where tree species composition and diet are likely different. In the second study, chimpanzee abundance in one type of habitat in Kalinzu Forest, Uganda, was not associated with fruit abundance in that habitat (chimp abundance actually increased while fruit abundance remained constant) because of the availability of a seasonal "fallback" food, making that habitat type important in the low-fruit season despite its overall low food availability. These studies emphasize the importance of detailed and comprehensive dietary information when assessing habitat quality for primates, especially when such information is to be used in planning conservation actions.

Various forest structural attributes not related to food availability have also been found to be important correlates of primate abundance. For many primates, these important attributes include number and size of trees. For example, density of *Presbytis entellus* in a forest in India was positively correlated with basal area coverage of trees and basal area coverage of trees and shrubs (measured as percent cover of 100m^2 plots) [Ross & Srivastava, 1994]. Skorupa [1986] found abundance of *Colobus badius* positively correlated with total basal area and *Cercocebus albigena* with total stem density across unlogged, lightly logged, and heavily logged plots in Kibale. In contrast, abundance of *Cercopithecus ascanius* was negatively correlated with basal area per stem and *Colobus guereza* with density of large (≥35cm diameter at breast height) stems. Skorupa [1986] also found that the abundance of *Cercopithecus l'hoesti* and *Pan troglodytes*, as well as the total primate index, was positively correlated with percent canopy (≥15m) cover. And in Medley's [1993] Tana River study, size of cut, dead, or damaged trees was negatively correlated with *Cercocebus galeritus* groups and individuals, while mean tree height, another measure of tree size, was positively correlated with the number of *Procolobus rufomitratus* groups and individuals and *C. galeritus* groups.

Finally, spatial attributes have also been investigated for their influence on primate numbers. Proximity or connection of the forest fragment to another forest is an important factor for *Alouatta palliata* [Estrada & Coates-Estrada, 1996] and *Macaca silenus* [Umapathy & Kumar, 2000b], but not for the presence/absence of five primates outside Kibale [Onderdonk & Chapman, 2000].

In the research to be presented here, a number of these previously identified factors are investigated with respect to their correlation with abundance of the Tana mangabey. These include forest area, basal area of the top 15 food species, basal area of their primary food species, density of sub-canopy and canopy trees, and area of canopy cover.

Behavioral and Ecological Flexibility

Research that encompasses the diversity of habitats a species occupies is important for investigating habitat needs of that species. In addition, studying primate behavior and ecology in a variety of habitats is critical to conservation, in that it provides understanding of the range of responses a species if capable of, as well as limitations to that range. For example, observing *Cebus apella* at the southern limit of its distribution, Brown and Zunino [1990] found that the species can subsist on bromeliads for the majority (72.3%) of their annual diet, a diet item that is eaten only occasionally (2.2%) at another site where *C. apella* has been studied. Another example comes from a study on the diets of *Colobus badius tholloni* and *C. angolensis* in Salonga, Democratic Republic of Congo (then Zaire), which found that both of these populations ate a higher proportion of seeds than other conspecific populations which have been studied [Maisels et al., 1994]. Such knowledge is important because it can help us to predict how and why a population adapts to, or does not survive, habitat alteration, degradation, and destruction, and can be used in management and conservation planning.

The key to understanding a species' behavioral and ecological flexibility is to link differences observed within a species to differences in the habitats that the different populations occupy. In the previously cited study, the southern population of *Cebus apella* had a diet dominated by bromeliads because there were few other resources available in that habitat [Brown & Zunino, 1990]. The Salonga colobines ate more seeds in congruence with the high prevalence of leguminous trees that predominate under conditions of poor soil quality at that site [Maisels et al., 1994].

This dissertation investigated the mangabey's ecological flexibility over long-term temporal and spatial scales; as such, the studies reviewed below are those that focus on these long-term (over one year) temporal and spatial factors. This excluded very short-term temporal differences such as seasonal changes [e.g., Mitani, 1989; Brugiere et al., 2002] or flexible foraging party size in one group [e.g., Chapman, 1990; Chapman et al., 1995; Phillips, 1995].

Perhaps the most important question to ask about a species' ecological flexibility is to what extent it can change its diet species and items. Such an ability will likely be a critical factor in whether a species will adapt to a new habitat as habitat degradation and destruction often impact primate diet species [e.g., Medley, 1993; White et al., 1995]. It is also a readily studied aspect of ecological flexibility, as species composition of tropical forests varies over international [e.g., Defler, 1996; Fleury & Gautier-Hion, 1999] and local [e.g., Butynski, 1990; Chapman & Fedigan, 1990] distances, and species composition and food availability vary across time [e.g., Norton et al., 1987; Olupot, 1998].

Long-term field studies often find that interannual variation in fruiting alone (without any changes in habitat) results in longer lists of diet species and items than those compiled from a single-year's study: *Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus* in Costa Rica [Chapman, 1987]; *Papio cynocephalus* in Mikumi National Park, Tanzania [Norton et al., 1987]; *Lophocebus albigena johnstoni* in Kibale National Park, Uganda [Olupot, 1998]; and *Procolobus badius* in Kibale [Chapman et al., 2002]. This speaks strongly to the value of longitudinal studies at single sites for a better understanding of a species' diet, which may be as critical to document as diet variation across different habitats.

Other changes in diet species or items can be attributed to temporal changes in plant species composition or density. For example, Olupot [1998] determined that in addition to interannual variation in fruiting, some of the diet differences observed in one group of *Lophocebus albigena johnstoni* over 20 years in Kibale may be attributed to longer-term temporal changes in composition and density at that study area, due to the increased area under softwood plantations and regenerating forest. On a much shorter "temporal" scale, in this case due to anthropogenic disturbance, *Hylobates lar* and *Presbytis melalophos* increased their intake of foliage after their habitats were selectively logged, which resulted in a lower fruit availability but a higher proportion of trees with new leaves [Johns, 1986].

Differences in plant species composition or density on a spatial scale can also result in dietary differences between populations. The high frequency of doum palm nut *Hyphaenae thebaica* in the diet of the Filoha, Ethiopia, population of *Papio h. hamadryas* is due to that diet species' high abundance in that particular study area [Swedell, 2002]. Chapman et al. [2002] attributed differences among eight sympatric groups of *Procolobus badius*, and even differences between two groups with overlapping ranges, to differences in species availability across the area of study. Likewise, Chapman and Fedigan [1990] studied the diets of three neighboring groups of *Cebus capucinus* in Costa Rica, and found that the different contributions of some plant items among the three diets could be explained by differences in presence/absence of the diet species among the home ranges of the groups.

Sometimes, however, temporal and spatial differences in diet species and items eaten cannot be explained by differences in species or item availability [Chapman, 1987; Chapman et al., 2002]. For example, only 19% of diet items that differed in the diets of three neighboring groups of *Cebus capucinus* were explained by availability differences; Chapman and Fedigan [1990] could not distinguish between the hypothesis of food profitability (maximum net energy yield per feeding time) and the hypothesis of local tradition (learned group traditions of recognizing and eating only certain foods) for the remaining diet items that differed among the three groups.

Ranging is another aspect of a species' behavioral and ecological repertoire through which populations can adapt to different habitats. On a temporal scale, the *Lophocebus albigena johnstoni* group in the Kanyawara study area of Kibale was studied in 1974 and again in 1991; between those years, the group expanded its range to include regenerating forest and exotic softwood plantations that had become available since the earlier study [Olupot et al., 1994]. Home range size can also differ between populations throughout a species' distribution. *Colobus satanas* groups in Forêt des Abeilles, Gabon, had much larger home ranges than groups studied in Lopé, Gabon, and Douala-Edéa, Cameroun [Fleury & Gautier-Hion, 1999]. The Forêt des Abeilles study site has a harsh main dry season and is dominated by the legume family Caesalpiniaceae. These plants do not produce fleshy fruit and irregularly produce seed, resulting in a low carrying capacity of the habitat and concomitant low population density and large home ranges for the colobus. Similarly, the group of *Lagothrix lagotricha* in the Colombian Amazon studied by Defler [1996] had a much larger home range than other groups studied elsewhere in the Amazon, possibly due to the study site's poor soils on which Sapotaceae dominated. The Sapotaceae produce hard-coated and leathery fruits with little flesh; the study group would therefore need to travel over a greater area to find sufficient nutrition.

Flexibility has also been observed in grouping patterns. Newton-Fisher et al. [2000] investigated the idea that chimpanzees in the Budongo Forest Reserve, Uganda, minimize feeding competition through their ability to change the size of their foraging parties [Wrangham, 1977, 1986]. Although they found a relationship between chimpanzee party size and patch size, they did not find a relationship between party size and habitat-wide measures of ripe fruit abundance. They argue that this lack of a relationship may be due to the study area's high abundance of food, and therefore that feeding competition's influence on chimpanzee party size will vary site-to-site and over time. A reverse relationship was observed when selective logging resulted in a low abundance of preferred food, and therefore a need for more intensive foraging, for *Presbytis melalophos*; groups adopted a system of group fissioning, which they did not engage in before logging [Johns, 1986]. Living in fragments, in contrast to continuous forest, may also influence grouping patterns. A *Cercopithecus cephus* group resident in a 9-hectare forest fragment in Lopé adopted a fission-fusion grouping pattern, perhaps due to the boundedness of the fragment, a central location to regroup, and lack of conspecific groups [Tutin, 1999].

In the research presented here, several of these aspects of primate flexibility, namely long-term temporal changes in behavior, diet, and ranging, are investigated in a group of Tana mangabeys, and attempts are made to link those changes to changes in the habitat.

Habitat Fragmentation and Primates' Responses to Fragmentation

As habitat destruction and degradation continue to be one of the main reasons for the endangerment of primates [Mittermeier & Konstant, 2002], the ecological study of habitat fragments and the responses of primates to fragmented environments will continue to be an important subject of inquiry. A forest fragment is not only a smaller area of forest, but also a drastically changed area of forest. As such, research has focused not only on area effects, but also on edge effects and matrix effects. These have been most extensively investigated in the Biological Dynamics of Forest Fragments Project (BDFFP), which was begun in 1979 to assess the effect of forest fragmentation on biodiversity in the Amazon [Bierregaard et al., 1992; Laurance et al., 2002].

As expected by the species-area curve devised by MacArthur and Wilson [1967], the number of animal species has been found to decrease and species extinction rates to increase with decreasing fragment size [Laurance et al., 2002]. Those animal species that are most impacted by small fragment size are those that require large home ranges [Bierregaard et al., 1992] and that are highly sensitive to a number of ecological aspects associated with fragment area, such as primates [Laurance et al., 2002]. The loss of certain guilds of organisms because of the small size of fragments (e.g., loss of predators of vertebrates) can alter the trophic web, resulting in densities of herbivores increasing and densities of seedlings and saplings of canopy trees decreasing [Terborgh et al., 2001]. This imbalance may eventually lead to a "biologically impoverished system" [Terborgh et al., 2001, p 1925]. The number of individuals per species present in a fragment also follows the species-area curve. Forest fragment size heavily influences the size of a population, and therefore its genetic variation and its ability to resist chance extinctions

[Saunders et al., 1991]. This contributed to Chiarello and de Melo's [2001] estimate that only Atlantic forest fragments greater than 20,000 hectares can support large enough populations of *Cebus apella*, *Callicebus personatus*, and *Callithrix geoffroyi* to evade extinction in the long term. Forest fragment size also impacts the plant community in the fragment, and hence food availability to herbivores. Tabarelli at al. [1999] found that the percentage of species dispersed by biotic instead of abiotic means was lowest in small fragments versus large fragments in the Atlantic forest of Brazil. More specifically, the percentage of species that are important providers of fleshy fruits for birds and mammals was lowest in small fragments.

When there is a forest fragment, there is also a forest edge. This edge, especially when abrupt and between two very distinct vegetations (as is often the case in the process of forest fragmentation), can have deleterious effects on the remaining forest, essentially further reducing the area of forest available to forest-living species [Murcia, 1995]. Edge effects on the forest arise because of differences between the two types of vegetation, and include changes in microclimate, forest structure, species assemblage, and ecosystem processes [Laurance et al., 2002]. Specific changes include invasion of disturbance-adapted species, changes in bird density, increased air temperature, reduced soil moisture, reduced canopy height, altered species composition of leaf-litter invertebrates, and elevated tree mortality [Laurance et al., 1997; Laurance et al., 2002]. Microclimate changes have been measured 15-60 meters into the fragment, while physical changes have been measured up to 400 meters into the fragment [Laurance et al., 1997; Laurance, et al., 2002]. Canopy trees greater than 60 cm diameter at breast height are especially prone to increased mortality as far as 300m from the fragment edge; this can heavily influence the frugivore community as large trees are sources of fruit for many animals [Laurance et al., 2000]. In addition, regeneration of shade-tolerant, mature-phase tree species has been found to be influenced more by edge effects than by area effects in Brazilian forest fragments [Benitez-Malvido, 1998].

The intervening matrix vegetation also affects forest fragments and species' ability to persist in them, leading Saunders et al. [1991] to call for integrated landscape management instead of management of the forest fragment alone. The type of matrix makes a difference; the BDFFP has found that edge effects are less pronounced in fragments surrounded by regrowth than in fragments surrounded by pasture [Laurance et al., 2002]. Distance of matrix between forest fragments is also critical in that many species have been found to avoid even clearings less than 100 meters across [Laurance et al., 2000]. Some species, including a number of primates, have never been observed to cross through the matrix of a fragmented habitat [e.g., *Macaca silenus*: Green and Minkowski, 1977, Umapathy & Kumar, 2000b; *Cercopithecus mitis labiatus*: Lawes et al., 2000]. For those species that can travel through corridors, recolonization is possible [Gascon et al., 1999; Laurance et al., 2002], as well as exchange of genetic material between sub-populations [Gascon et al., 1999], and the use of resources of different fragments [Tutin et al., 1997]. The ability of a species to actually use the varying matrix in a fragmented habitat can also influence its survival in fragments. Gascon et al. [1999] found that the ability of birds, frogs, and small mammals to use the matrix in a fragmented habitat in the Amazon was correlated with stable or increasing populations in the forest fragments. This effect is one that certainly should be more extensively investigated for primates.

Unfortunately, there are very few studies that have statistically investigated correlations between characteristics of species and their ability to persist in modified habitats, and those few studies are not readily comparable because of differences in the type of habitat modification studied. Onderdonk and Chapman [2000] found that none of the four species characteristics investigated – home range size, body size, group size, and degree of frugivory – predicted the ability of six species to live in forest fragments outside Kibale National Park, Uganda. In contrast, Fimbel [1994a] found that percent frugivory, along with small body size, was correlated with density of six primates in regenerating farm clearings adjoining old forest on Tiwai Island, Sierra Leone. Mean group spread, group biomass, group size, and percent terrestriality were not correlated with use of the habitat matrix. Both studies argue that a primate's response to habitat modification and fragmentation is site-specific, and caution should be taken when attempting to generalize between sites and species. Skorupa [1986] has also investigated correlations between socioecological variables and vulnerability to habitat disturbance (proportional difference between a primate species' abundance in undisturbed and selectively logged forest), finding home range area, group spread, and percent of fruit, seeds, and flowers to be positively correlated with vulnerability.

Descriptive, post-hoc explanations of patterns of persistence across species are more common in the literature. Contrary to Onderdonk and Chapman's [2000] finding that species' home range sizes did not predict their ability to live in patches, several other studies have hypothesized that home range size does influence presence in fragments. For example, *Ateles paniscus* and *Chiropotes satanas* in Brazil [Rylands & Keuroghlian, 1988] and *Macaca silenus* in India [Umapathy & Kumar, 2000b] are excluded from smaller fragments because of their large home ranges. The need for a large home range may be due to the patchy distribution of fruit, and therefore frugivores will be more affected by small fragment size than folivores. The frugivores *Cebus apella*, *Callicebus personatus*, *Callithrix geoffroyi*, and *Alouatta fusca* are found at lower densities in smaller fragments of Brazilian Atlantic forest [Chiarello & de Melo, 2001]. On the other hand, *Alouatta palliata*'s high degree of folivory and *A. seniculus*' ability to eat foliage have been cited as an important reason for those species' persistence in forest fragments [Lovejoy et al., 1986; Estrada and Coates-Estrada, 1996; Estrada et al., 1999]. Sample effects, the chance that a patchily distributed species is present at fragment creation, has been found to be important for several species [Laurance et al., 2002], and may be applicable to rare primates [e.g., *Pithecia pithecia*: Lovejoy et al., 1986].

Flexibility in diet, ranging, and grouping also appears to play a role in a species' ability to survive in a fragmented habitat. The diets of *Cercopithecus cephus*, *Cercopithecus nictitans*, *Lophocebus albigena*, *Colobus satanas*, and *Pan t. troglodytes* differed between continuous forest and a 9-hectare fragment in the Lopé Reserve, Gabon [Tutin, 1999]. Overall, the species ate more insects, leaves, and petioles, and fewer flowers, fruit, and seeds in the fragment. A group of *Alouatta fusca* in a 250-ha fragment in Brazil ate a similar proportion of leaves as groups studied elsewhere, but a greater proportion of leaves came from liana species, which were much more common in the fragment [Chiarello, 1994]. Singh et al. [2001] observed a group of *Macaca silenus* living in a forest fragment on a coffee-tea estate in south India acquiring more of their diet from non-native, weed, and cash crops (39.9% of feeding observations) than from native species (36.7%).

Ranging behavior can also differ between groups living in fragments and continuous forest. Considering that the need to range over a large home range may limit the ability to persist in fragments, the ability to be flexible in home range size may be critical to those species. The home range of a *Cercopithecus cephus* group resident in a 9-hectare fragment was observed to be much smaller than that species' typical home range size of 75-100 hectares in continuous forest [Tutin, 1999], and *Cercopithecus pogonias* groups that are resident in fragments have also been reported to have home ranges 8-25 times smaller than those in continuous forest [Tutin et al., 1997]. Although these species' abilities to travel through the intervening savanna [Tutin et al., 1997] to visit forest fragments would allow groups with large home ranges to visit fragments, their flexibility in home range size certainly allows them to be resident in the fragment.

Finally, flexibility in grouping patterns or in group size may also play a role. The *Cercopithecus cephus* group resident in the 9-hectare fragment in Lopé that had a different diet and a smaller home range than groups in continuous forest also developed a fission-fusion pattern of foraging, which it does not do in continuous forest [Tutin, 1999]. It was thought that the distinct boundaries of the fragment, the presence of a highly preferred "safe place" at which the group could regroup, and the absence of neighboring conspecific groups allowed for this pattern of grouping. The group of *Macaca silenus* in the 65-hectare fragment that had a smaller home range also had a larger group size than in nearby continuous forests [Menon & Poirier, 1996]. Because two smaller groups would have overlapping home ranges in the small fragment, remaining in one large group would avoid intergroup conflict. A similar effect was noted for *Alouatta pigra* groups in 44 forest fragments near Chiapas, Mexico. These fragment groups had a smaller mean troop size than groups in nearby continuous forest, although it was within the range of mean group size found in other undisturbed sites [Estrada et al., 2002]. A healthy proportion of infants in the fragment groups also implied that although the groups were small, they were continuing to reproduce effectively.

The issues discussed above that will be incorporated into or addressed by the research presented here include the Tana mangabey's use of the matrix habitat, its movement between forest fragments, and its ecological flexibility that allows it to survive in a fragmented habitat.

Tana River Study Area

The lower Tana River, Kenya (Fig. 1), provides a context that is highly suited to the study of the ecological correlates of primate abundance, behavioral and ecological flexibility of primates, and primates' responses to habitat fragmentation. The Tana River is Kenya's longest river, flowing from the Mount Kenya region to the Indian Ocean near Kipini. The lower Tana River (defined here as 1°40' to 2°15' S, 40°07' E, the 60 kilometer distribution of *Cercocebus galeritus*) flows through an arid/semi-arid area. Mchelelo Research Camp, located within the Tana River Primate National Reserve (TRPNR), receives a mean annual precipitation of only 582 mm (averaged by month for 38 months 1996-2001; unpublished climatological data, Mchelelo Research Camp). The Garsen area, at the southern limit of the mangabey's range, receives 600 mm per year [Hughes, 1990]. Rainfall occurs in two rainy seasons: the short rains of November and December, and the long rains of March through June. The mean daily minimum temperature is 23.1°C and the mean daily maximum temperature is 32.9°C, measured at Mchelelo Research Camp (unpublished climatological data).

The lower Tana River supports roughly 62 forest fragments, ranging in size from 1 to 408 hectares. These forests are found along the river channel, which they rely on for their survival. The forests are classified as floodplain forest, dependent on the Tana River's processes of flooding and nutrient recharge and the height of the groundwater table [Hughes, 1990], instead of local precipitation. Because they are especially dependent on the extent of the groundwater table, forests are limited to within approximately 1 kilometer on either side of the river. The height of the river flow is dependent on precipitation in the headwaters. Biannual floods of the river generally occur in May and November, although they have been severely dampened recently due to upstream dams [Hughes, 1990] and droughts in Kenya.

The lower Tana River supports approximately 175 woody plant species, a unique combination of Zanzibar-Inhambane (East African coastal), Guinea-Congolian (West and Central African), Somalia-Masai (northeastern), Zambezian (southern), and pan-African species [Medley, 1992]. There are two species endemic to the lower Tana River, *Coffea s. sessiliflora*, and *Pavetta sphaerobotrys tanaica*. *Populus ilicifolia* is endemic to riverine forests in Kenya. *Cynometra lukei* in Kenya is found only along the Tana River but is also found in Tanzania. In addition, *Pachystela msolo* is found outside West Africa only along the Tana and in Tanzania. The high percentages of pan-African and Guinea-Congolian plant species are evidence of a once more continuous distribution of evergreen forests across Africa. The high percentage of species of the Zanzibar-Inhambane region, however, suggests a rather lengthy isolation and speciation apart from the West and

Central African forests. The continuous evergreen forest belt between the Congo basin and the East African coast was most likely present only during wetter periods in the Pleistocene (31,000-26,000 and 8000 BP) [Medley, 1992].

Due to the dynamics of the river, the individual forest fragments are highly inconstant. The Tana River is a meandering river, and forest area may be lost as the faster river flow on the outside banks results in erosion. As the outside bank is eroded, however, the slower moving water on the inside bank deposits sediments, forming point bars [Seal & MacDonald, 1991]. Occasionally, especially during floods, river meanders may be cut off, forming ox-bow lakes, and the river may change course. As a result, forests become isolated from the groundwater table and the nutrients of floodwaters, and forest senescence will eventually occur; along the new river course, however, floodplain forest may develop [Hughes, 1984]. The forests are also extremely heterogeneous, evidenced by distinctive forest types as well as highly unstable plant composition. Based on vegetation associations, soil types, flooding frequency, and position in reference to the river, Hughes [1988] classified the Tana River vegetation into seven forest types. Across 12 forest fragments within a 30-kilometer stretch of one side of the river, Medley [1990] found community similarity of relative coverage of canopy trees to range between 4.7% and 84%.

In addition to river dynamics, the local human population also adds to the dynamism and heterogeneity of forest fragments. The local agriculturalists slash and burn forest for farmland. As forests establish themselves on the most productive soils, that land is also the most valuable for farmland. Although the cutting of indigenous forest is prohibited by law, forest loss to clearing has recently increased to an estimated

30% of the minimum total forest area in the lower Tana River in 1994 [Wieczkowski & Mbora, 1999-2000]. The local people also depend on the forest for various forest products. The most destructive activities are the felling of canopy trees to construct canoes and beehives, and to collect wild honey; harvesting of palm fronds to make thatching and mats; cutting of sub-canopy trees to use as housing poles; and topping of the *Phoenix reclinata* palm to collect palm wine. In 2000, 12 fragments in the northern half of the study area were classified as suffering from heavy, very heavy, or extreme human use [Wieczkowski & Mbora, 1999-2000].

The lower Tana River is also habitat for more than 260 bird species and 57 mammal species [Andrews et al., 1975]. BirdLife International classifies the lower Tana River as an Important Bird Area because of the diversity of species, and the presence of globally threatened, regionally threatened, and range-restricted species [Bennun and Njoroge, 1999]. The area is habitat for the endangered African elephant (*Loxodonta africana*) and the endangered hirola (*Beatragus hirola*). The forests of the lower Tana River also are considered the most important primate conservation area in Kenya, if not in East Africa [Kenya Section of the IUCN/SSC Primate Specialist Group and the Kenya Primate Conservation Group, 2000]. The forests are habitat for seven non-human primate species: the Tana mangabey (*C. galeritus*), Tana River red colobus (*Procolobus rufomitratus*), Sykes monkey (*Cercopithecus mitis albotorquatus*), yellow baboon (*Papio c. cynocephalus*), Zanzibar galago (*Galago zanzibaricus*), Senegal galago (*G. senegalensis*), and Garnett's galago (*Otolemur garnettii*). In addition, the bush and grasslands are habitat for the vervet monkey (*Cercopithecus aethiops pygerythrus*) [Butynski & Mwangi, 1994]. The mangabey and red colobus are CITES Appendix I taxa

[IUCN, 1996], classified as critically endangered [IUCN, 2000], and are on the list of the top 25 most endangered primate species [Mittermeier & Konstant, 2002]. In addition, the Zanzibar galago is classified as vulnerable and the Sykes monkey is a regional endemic [Butynski & Mwangi, 1994].

The Tana mangabey has been the subject of several population censuses and two extensive socioecological studies (dissertations). Earliest censuses in 1975 estimated the mangabey population to be between 1,100 and 1,500 individuals [Marsh, 1986]. By 1986, however, the mangabey population was found to have declined by 25%, to 800-1,100 [Marsh, 1986]. The decline in the population was most likely due to forest senescence [Marsh, 1986; Medley, 1990] and/or loss of forest area to clearance for farmland and to river course changes [Decker, 1989; Medley, 1990]. The most recent and most intensive census estimated the population at 1,000-1,200 [Butynski & Mwangi, 1994].

The first systematic research on the mangabey was Homewood's [1976] study in two forest fragments of this diverse system. One fragment was zoned, with areas of flooding, transitional, and monospecific evergreen forest types, and with limited species diversity. It supported an intermediate mangabey density. The other was a diverse multi-species evergreen forest with a very high mangabey density. Homewood studied how mangabeys shift their "patterns of exploitation" in response to seasonal and local differences in their habitat. The study groups were flexible in their grouping patterns, forming sub-parties when food resources were scarce and peacefully aggregating when food resources were abundant. The mangabeys were also flexible in their diet choices; they concentrated on the diet species that were most abundant at the time and increased the species diversity of their diet as food availability decreased. One study group was also able to take advantage of fruit production by one diet species by temporarily moving to another forest fragment, where that species was locally abundant. Homewood concluded that this ecological flexibility in grouping, diet, and ranging allowed them to survive in the fluctuating environment of the lower Tana River.

Kinnaird [1990] compared Homewood's data from fifteen years prior to her own to study how mangabey diet had changed as a result of large-scale habitat changes (forest loss and fragmentation due to river changes and extensive clearance of forest for agricultural land) and subsequent declines in diet species. These inter-year comparisons, as well as seasonal differences within Kinnaird's field season, provide further support for ecological flexibility. The study groups had increased their intake of unripe seed, perhaps responding to a decrease in ripe fruit availability between the two studies. Two adjacent mangabey groups that Kinnaird observed also showed flexibility in intergroup interactions, avoiding one another when fruit abundance was low, merging into non-aggressive associations when fruit abundance was high but distribution was uniform, and engaging in aggressive encounters when fruit abundance was high but distribution was patchy. Kinnaird suggested that these mangabeys may be able to "compensate for permanent loss of habitat and critical food resources" [Kinnaird, 1990, p. 249].

Conservation of the forests and primates of the lower Tana River has not been very successful, as evidenced by the recent increase in forest clearing and product use, and failure of a US$6.2 million World Bank-funded Global Environment Facility (GEF) project [Wieczkowski & Mbora, 1999-2000]. In 1976, the Kenya government gazetted 169 km^2 as the Tana River Primate National Reserve (TRPNR) to protect the red colobus, mangabey, and their forest habitat [Homewood and Mkunga, 1977; Fig. 1.1]. Because it was the Tana River County Council who requested the Ministry of Tourism and Wildlife to gazette the reserve (letter from Clerk Tana River County Council to Permanent Secretary Ministry of Local Government, 9 July 1974; TRCC/F.3/(165)), the TRPNR is officially a County Council Reserve. As such, the Tana River County Council should be the reserve's managers and should receive all economic benefits accruing from the reserve. From the beginning, however, the County Council requested that the national wildlife management organization manage the TRPNR on the County Council's behalf (letter from Acting Clerk/Treasurer Tana River County Council to Permanent Secretary Ministry of Local Government, 15 November 1974). The Kenya Wildlife Service (KWS), therefore, is the current manager of the TRPNR.

The main management concern of the TRPNR since gazettement has been the presence of people farming and living within its borders. Although the Tana River County Council passed a resolution shortly after gazettement that stated all people within the Reserve must leave by 1983 and would be compensated by the government (letter from Jim Else, National Museums of Kenya, to Director, Wildlife Conservation and Management Department, 4 May 1989), not everyone left and those that did were never compensated. Subsequently, in 1991, a population and habitat viability assessment (PHVA) was undertaken [Seal et al., 1991], concluding that in order to protect the lower Tana River in the long-term, the people farming and living within the TRPNR would have to be removed [World Bank, 1996].

The 1991 PHVA was the first step of the World Bank-funded US$6.2 million Tana GEF Project. This project ran from 1996-2001 and included three components:

Reserve Management, Research and Monitoring, and Community Conservation and Development. The objective of the GEF Project was conservation of the biodiversity of the lower Tana through improved management. As per the recommendations of the PHVA, one of the project's exercises was the relocation of families within the TRPNR to land outside the area of conservation concern [World Bank, 1996]. The initial proposal, however, was for forced eviction, which was obviously not accepted by the local people. In the end, the project was to encourage people to voluntarily relocate.

This relocation exercise became the focus of the entire GEF Project, and ultimately its demise. The result of the emphasis on relocation was delayed implementation of the Reserve Management and Research and Monitoring components; neglect of enforcement patrols, ecological monitoring, and dialogue with the community; mistrust and misunderstanding on the part of the local people (both those involved with and outside the Project); and a severe escalation in forest clearing [Mbora, 2000a, 2000b]. The Tana GEF Project ended in 2001 with very few conservation goals achieved and not a single person relocated.

In reality, however, successful conservation of the lower Tana River requires more than the protection of the forests and primates within the Tana River Primate National Reserve. The most important reason for this is that the reserve is too small to effectively conserve the biodiversity of the lower Tana River. The reserve protects only 56% of the mangabey groups and 37% of the colobus groups. In addition, only 48% of the forests with mangabeys and 32% with colobus are within the reserve, and as such, significant percentages of both critically endangered primates and their forest fragments are unprotected [Butynski & Mwangi, 1994]. This was noted as early as 1991 when the

PHVA concluded that the reserve was not large enough for the long-term persistence of the red colobus [Captive Breeding Specialist Group, 1991]. This inadequate protection extends to the diverse flora, as well; Medley [1990] has documented that the regional diversity of forest types and woody plant species in the lower Tana River is not protected within the reserve as it is currently demarcated. All of this is compounded by the forest clearance that occurred as a result of the Tana GEF Project's focus on one management issue within the reserve (relocation of the human population), and it illustrates what can happen when an ecosystem approach is not taken. The fact that Nkanjonja forest, a forest that was considered the best site for potential relocation of endangered red colobus groups and was habitat for 8% of the mangabey population [Butynski & Mwangi, 1994], was completely cleared because of the GEF Project [Mbora, 2000a] is especially devastating for the conservation of the critically endangered primates.

Dissertation Overview

This dissertation is written in the manuscript format; each of the successive chapters is a manuscript that I have prepared for submission to academic journals. Although each manuscript is independent, together they form a coherent whole in addressing the overall aim of this dissertation, to investigate the Tana mangabey's use of a fragmented habitat within the context of its ecological flexibility. Each manuscript addresses a component of this research question and is briefly introduced here.

The first manuscript (second chapter), "Ecological correlates of abundance in the Tana mangabey (*Cercocebus galeritus*)," investigates the ecological correlates of abundance in the mangabey with the goal of recommending management strategies from the results. I collected forest attribute and mangabey abundance data in 31 forests throughout the 60-kilometer distribution of the mangabey. Combining these two data sets allowed me to determine what forest attributes were most responsible for variation in mangabey abundance across these forest fragments. The explanatory variables tested were derived from existing research; they are forest area; food availability measures composed of basal area of the top 15 food trees per hectare, basal area of *Phoenix reclinata* per hectare, and basal area of *Ficus sycomorus* per hectare; forest structural measures of mean tree height, density of trees, basal area per hectare, and area of canopy cover per hectare; and forest disturbance measures of basal area of harvested trees per hectare and basal area of harvested *P. reclinata* per hectare. Because mangabeys are able to travel through the matrix habitat to visit neighboring forest fragments, I surveyed fragments on several occasions in order to account for this ability. As previously discussed, studies of this kind can play an invaluable role in primate conservation, providing information on what specific areas and habitat attributes management should focus on.

The second manuscript (third chapter), “Temporal comparisons of behavior and diet in a Tana mangabey (*Cercocebus galeritus*) group,” and the third manuscript (fourth chapter), “An examination of the increased annual range of a Tana mangabey (*Cercocebus galeritus*) group,” are further contributions to assessing the ecological and behavioral flexibility of the mangabey. The study group is one that had also been the focus of research by Homewood [1976] and Kinnaird [1990], so my investigation extends our long-term data collection on this group and allows for an examination of their flexibility on an expanded temporal scale. Behavioral and dietary changes are investigated in the first of these two manuscripts, while expansion of the group's home range and the correlation of that change to alteration of the group's habitat over the same time period, is the focus of the final manuscript. Once again from the perspective of conservation of this and other endangered species, improved understanding of a species' ecological and behavioral flexibility should permit predictions of how particular species will respond to habitat changes, and hence our ability to manage primate habitats.

Specific methods and statistical analyses appropriate to each aspect of the overall study are presented in the individual manuscripts. Here, I will present a summary overview of the general methods.

Forest attribute and mangabey abundance data

The study utilized vegetation attribute and mangabey abundance data collected in 31 of the 62 forests in the lower Tana River. These forests were chosen to sample those with and without mangabeys, on the west and east bank of the river, and inside and outside TRPNR. Additional considerations of location, need for security, extreme current forest clearance, community opposition, and the concurrent study on the Tana River red colobus undertaken by David Mbora were also taken into account.

In each forest, I randomly established three belt transects of 100 meters long by 5 meters wide. For larger forests, the log was taken of the forest area and an additional belt was sampled for every one log unit. The belt transects were alternatively established at the forest's edge, the river, and the middle of the forest, in order to sample across the groundwater gradient. Within each belt transect, I collected species, height, and diameter at breast height (DBH) of each tree ≥ 10 cm DBH. Four of the mangabey's top 15 food species reproduce at sizes less than 10 cm DBH. For *Saba comorensis*, *Oncoba spinosa*, and *Polysphaeria multiflora*, I recorded the species and height of each individual that showed evidence of reproduction (fruits, flowers, or visible remains); for *Phoenix reclinata*, I recorded individuals that had an obvious trunk. Cut stems and branches greater than 10 cm diameter were identified and the diameter was measured where cut. *Phoenix* individuals with obvious trunks suffering ≥ 50% removal of the fronds or topping of the stem were recorded as harvested. A black and white photograph was taken of the forest canopy every 20 meters along the transect and continuing to the edge of the forest. Forest area was measured from the most recent aerial photographs of the area, taken in 1994 and 1996.

In each forest, I also surveyed for the presence of mangabeys using a modification of the quadrat census method [National Research Council, 1981]. Because of the mangabey's ability to move between forest fragments, I attempted to survey each forest monthly.

Mangabey socioecological data

The Mchelelo West group of mangabeys, which uses Mchelelo West forest, Mchelelo Research Camp, and Guru South forest, was the focus for investigation of the mangabey's behavior, ecology, and ranging. This group was chosen because it had been studied by both Homewood [1976] and Kinnaird [1990] in the previous two extensive investigations, and its study would therefore continue the long-term data collection on the group. I followed the group for a total of 12 3-day samples, from August 2000 until July 2001. The group was continuously followed from 0700 to 1815 hours during each day of each sample.

Every half hour, I conducted a 10-minute scan sample [Altmann, 1974]. For each individual mangabey observed, I recorded: first behavior sustained for five seconds, and if eating or foraging, species, diet item, and stage of ripeness. Behavioral categories recorded were eat, forage, move, social/sexual (e.g., allogroom, copulation, vocalize), inactive, and other.

After the ten-minute scan sample, I spent five minutes recording the location of each mangabey on maps drawn of the study area. Areal ranging data were calculated by superimposing a 50 meter by 50 meter grid on the maps. Center-of-mass of the group was calculated as the center of a polygon drawn around all visible individuals during each 5-minute mapping sample [Waser & Floody, 1974]. A total home range was calculated for the group as the number of unique quadrats entered during the entire study.

Phenology

To examine the mangabeys' behavior, ecology, and ranging in relation to food availability, I collected phenological data on the day immediately prior to and following each 3-day follow. I sampled 226 individual trees from 11 species across the three forested areas used by the group. I selected species in each of the three areas based on their importance in the mangabey diet and on their abundance in each area. The top 15 diet species (excluding fungi, animal matter, and grass) were determined from average percent contributions of each species to the mangabey diet [based on five groups: Homewood, 1976; Kinnaird, 1990]. The nine most abundant of these fifteen species were selected per area. For most species, ten individuals were monitored; for species whose populations did not include ten individuals, all individuals present were monitored. The presence of unripe and ripe fruits was scored on a 0-5 scale [Homewood

1976]. The diameter at breast height (DBH) of each tree in the phenology sample was also measured.

CHAPTER 2

ECOLOGICAL CORRELATES OF ABUNDANCE IN THE TANA MANGABEY (*Cercocebus galeritus*)[1]

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[1] Wieczkowski, J. To be submitted to *American Journal of Primatology*.

ABSTRACT

This study 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 from the results. Thirty-one study forests were chosen throughout the mangabey's 60-km distribution along the lower Tana River in southeastern Kenya. Within these study forests, 107 belt transects were sampled (mean per forest = 3.45; SE = 0.185; range 2-6) and 370 mangabey surveys were conducted (mean per forest = 11.94; SE = 1.623; range 1-31). A weighted multiple regression analysis was applied to determine if there is dependence between selected forest attributes and mangabey abundance. Forest area and density of trees ≥ 10 cm DBH were the only variables to significantly correlate with the variation in mean number of mangabey groups per forest. No additional variables were significant when the analysis was limited to forests inside the Tana River Primate National Reserve (TRPNR) or to forests outside the TRPNR. When human forest product use was accounted for, an additional variable, total basal area of the top 15 food species, correlated significantly with variation in mangabey abundance within the TRPNR. Management, therefore, should focus on increasing forest area, density of trees ≥ 10 cm DBH, and coverage of food trees throughout the mangabey's distribution. There is also a need to collect dietary data from additional mangabey groups, especially those towards the southern limit of the mangabeys' distribution where plant species composition differs from forests in which dietary data have been previously collected. Solutions must be found to forest clearing, and forest product use must be better managed to protect the habitat of this critically endangered primate.

Key words: mangabey (*Cercocebus galeritus*); forest attributes; management; endangered primate; forest product use; abundance

Short title: Ecological correlates of mangabey abundance

INTRODUCTION

One of the most serious threats to the majority of the 195 threatened non-human primate species and sub-species is habitat destruction [Mittermeier & Konstant, 2002]. As habitat degradation and destruction occur on a larger and larger scale, it becomes imperative, as a first step towards conserving primates, to understand the relationship between primates and their habitats [Schwarzkopf & Rylands, 1989; Medley, 1993b; Reed & Fleagle, 1995; Estrada & Coates-Estrada, 1996; Balcomb et al., 2000; Onderdonk & Chapman, 2000]. It is critical to understand the habitat attributes that are most important in supporting primate species prior to and/or subsequent to habitat change. This understanding can then be used to recommend management and conservation strategies, or may be integrated into long-term conservation plans for the primates and their habitats [Medley, 1993b; Fimbel, 1994; White et al., 1995; Estrada & Coates-Estrada, 1996; Rosenbaum et al., 1998; Balcomb et al., 2000; Chapman & Lambert, 2000; Sorensen & Fedigan, 2000; Stevenson, 2001; Chapman et al., 2002]. In addition, as habitat degradation and destruction occur on a larger and larger scale, the study of the remaining forest fragments [Saunders et al., 1991; Laurance et al., 1997; Laurance et al., 2002] and the ability or inability of primates to use those fragments [Tutin et al., 1997; Tutin, 1999; Bobadilla & Ferrari, 2000; Onderdonk & Chapman, 2000; Mbora, 2003] becomes increasingly important.

The Tana mangabey (*Cercocebus galeritus*) is endemic to a chain of forest fragments along a 60-kilometer stretch of the lower Tana River in Kenya. These forest fragments are discrete and both naturally and anthropogenically created [Hughes, 1990; Medley, 1990], providing an opportunity to study the mangabeys' habitat requirements and use of forest fragments. In addition, the Tana mangabey is classified as 'Critically Endangered' [IUCN, 2000] and one of 'The World's Top 25 Most Endangered Primates' [Mittermeier & Konstant, 2002]; it is most threatened by habitat loss. Only 47% of forests with mangabeys and 56% of mangabey groups are found within the protected Tana River Primate National Reserve (TRPNR) [Butynski & Mwangi, 1994]. Recent research has found a 30% loss in forest area and a high level of forest degradation within the distribution of this primate [Wieczkowski & Mbora, 1999-2000]. With a population last reliably estimated at only 1,000-1,200 individuals [Butynski & Mwangi, 1994], the long-term survival of the Tana mangabey is seriously endangered. Long-term conservation plans for this species must be informed by an understanding of their habitat requirements.

Medley [1993b] looked at ten forest attributes in order to determine what constitutes "suitable" habitat within the Tana River Primate National Reserve for the critically endangered and endemic Tana River red colobus (*Procolobus rufomitratus*) and the mangabey. The number of mangabey groups and individuals were each significantly negatively correlated with basal area of cut, dead, or damaged stems and intraforest heterogeneity, and significantly positively correlated with area-to-perimeter ratio. In addition, the number of groups was significantly positively correlated with mean canopy height, whereas the number of individuals was significantly positively correlated with

Phoenix reclinata density. Medley [1993b] concluded that both Tana primates would benefit from conservation of high-stature, closed canopy forest with a high area-to-perimeter ratio and little forest disturbance.

In this study, I investigated the ecological correlates of abundance in the Tana mangabey with the goal of recommending management strategies from the results. The variables examined included forest structural, mangabey food resource, and human forest product use attributes. The attributes, and their hypothesized relationships to mangabey abundance, are the following.

- Forest area.

  Many of the mangabeys' important food resources have clumped distributions and occur at low densities [Kinnaird, 1990; Medley, 1990]. A larger forest will provide more of these resources and should support a higher mangabey abundance.
- Density of trees, Mean tree height, Tree basal area, and/or Area of canopy cover.

  The mangabey requires an arboreal habitat from which to feed, and in which to sleep and to take refuge [Homewood, 1976; Kinnaird, 1990]. A forest with a higher density of trees, higher mean tree height, larger tree basal area, and/or larger area of canopy cover will provide a more suitable arboreal habitat and should support a higher mangabey abundance.
- Basal area of the mangabeys' top 15 food species.

  A forest with a larger basal area of the top 15 food species should support a higher mangabey abundance.

- Basal area of *Phoenix reclinata*.

  P. reclinata is classified as a critical mangabey food resource [Kinnaird 1990, 1992] and is their primary food species [Homewood, 1976; Kinnaird, 1990]. A forest with a larger basal area of *P. reclinata* should support a higher mangabey abundance.
- Basal area of *Ficus sycomorus*.

  F. sycomorus is classified as a critical mangabey food resource [Kinnaird 1990, 1992]. A forest with a larger basal area of *F. sycomorus* should support a higher mangabey abundance.
- Basal area of harvested trees.

  Many of the most common species that humans cut for canoes, beehives, and poles [Gachugu 1992; Kahumbu 1992; Medley 1993a] are also important food resources for the mangabeys [Homewood 1976; Kinnaird 1990]. In addition, harvesting of trees impacts forest structure. A forest with a smaller basal area of harvested trees will provide more resources, and should support a higher mangabey abundance.
- Basal area of harvested *P. reclinata*.

  P. reclinata is the most widely used palm species by humans along the Tana River [Gachugu 1992; Kinnaird 1992; Medley 1993a]. A forest with a smaller basal area of harvested *P. reclinata* will provide a higher abundance of this resource, and should support a higher mangabey abundance.

Medley's [1993b] work was improved upon in several ways. I attempted to account for movement of mangabey groups among forests, which better reflects true abundance in each forest - something that Medley [1993b] did not do. In addition, I expanded the study of the mangabeys' habitat to include additional forest attributes, such as basal area of *Ficus sycomorus*, and a more detailed study of human forest product use. I also measured abundance of the top food species more accurately through use of a list of the mangabeys' top 15 food species; Medley [1993b] combined important colobus and mangabey food species into one measure in her study. The study was also expanded to include forests on the east bank of the Tana River, and in the area to the south of TRPNR. There has been no previous systematic work in forests on the east bank and outside the TRPNR [but see Mbora, 2003] and as such, research in these forests greatly increases our understanding of the diversity of the Tana River system. Forest composition is known to differ between forests within and outside the TRPNR [Medley, 1992], which suggested that forest structure and human impact might differ as well. This study allowed comparisons between these forest areas and determination of whether the ecological correlates of mangabey abundance differed between the two subsets of forests. Finally, I performed a weighted multiple regression analysis [Neter et al., 1985] to analyze the relationships between the forest attributes and mangabey abundance, in contrast to Medley's [1993b] use of correlation. Multiple regression analysis has several major advantages over correlation, especially when the results will be used in management decisions. These include determination of the relative contribution of each significant independent variable to variability in the dependent variable and prediction about new samples from the same population [Crown, 1998; Harris, 1998].

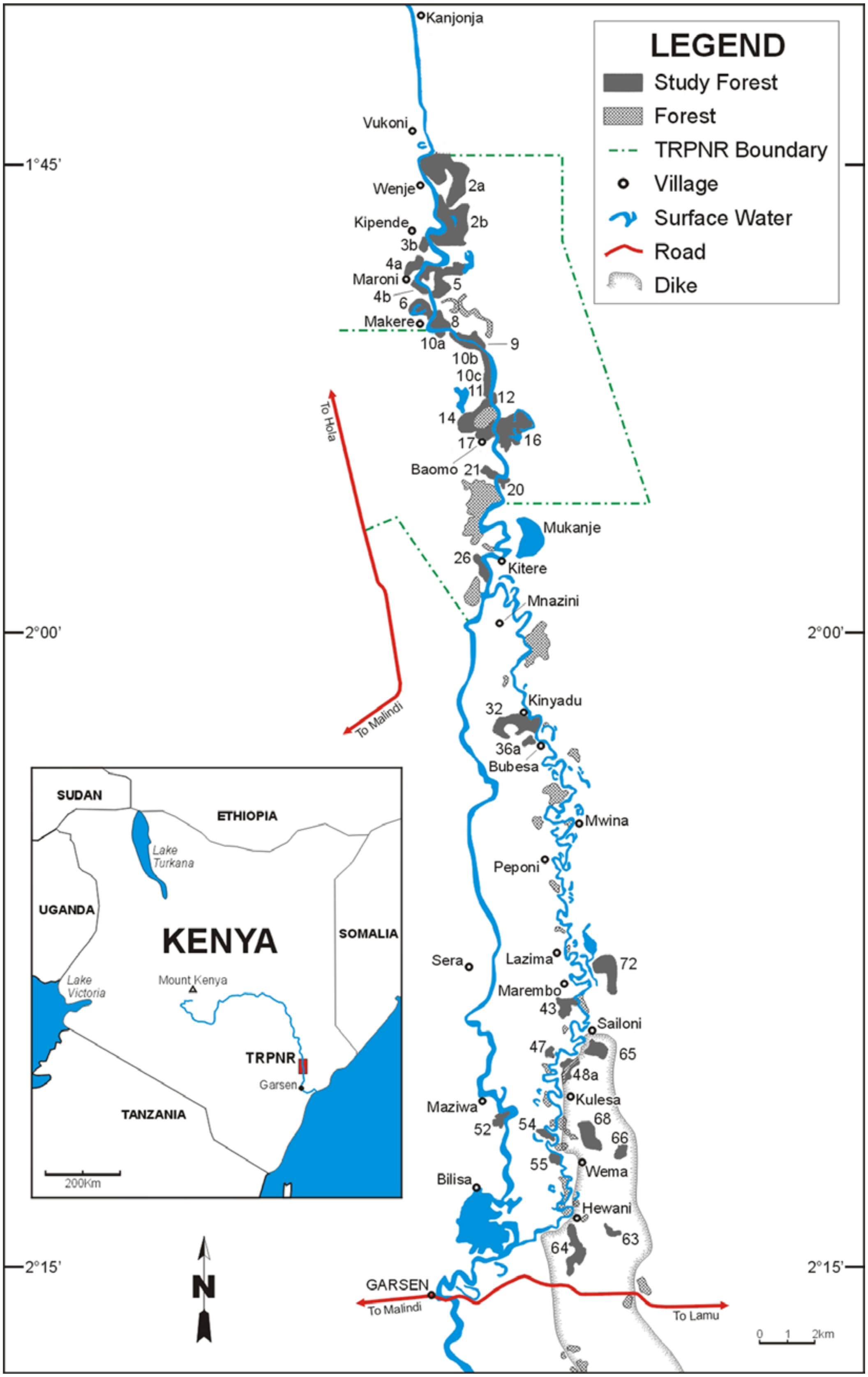
METHODS

Study Area

The study was undertaken within the 60-kilometer distribution of the Tana mangabey along the lower Tana River, Kenya (1°40’ to 2°15’ S, 40°07’ E) (Fig. 2.1). The lower Tana River supports roughly 62 forests [Butynski & Mwangi, 1994; Mugo, 1996; per. obs.]. These are classified as riverine forest and are dependent on the Tana River’s processes of inundation, sediment transport, erosion, alluvial deposition, and groundwater level [Medley, 1990]. In fact, the lower Tana River is an arid/semi-arid area, receiving a mean annual precipitation of 582 mm (averaged by month for 38 months 1996-2001; unpublished climatological data, Mchelelo Research Camp). Rainfall occurs in two rainy seasons: the short rains of November and December, and the long rains of March through June. The mean daily minimum temperature is 23.1°C and the mean daily maximum temperature is 32.9°C (unpublished climatological data, Mchelelo Research Camp).

The forests of the lower Tana River support more than 57 mammal species, 260 bird species, and 175 woody plant species [Andrews et al., 1975; Medley, 1992]. The lower Tana River is especially important for primate conservation, providing habitat for eight non-human primate species: the Tana River red colobus (*P. rufomitratus*), the Tana mangabey (*C. galeritus*), Sykes monkey (*Cercopithecus mitis albotorquatus*), vervet monkey (*Cercopithecus aethiops pygerythrus*), yellow baboon (*Papio cynocephalus cynocephalus*), Zanzibar galago (*Galago zanzibaricus*), Senegal galago (*Galago senegalensis*), and Garnett’s galago (*Otolemur garnettii*) [Butynski & Mwangi, 1994]. In addition to the critically endangered and endemic red colobus and mangabey, the

Fig. 2.1. The 60-kilometer 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 forests. Study forests are named and numbered as follows [following Butynski & Mwangi, 1994]: Wenje East (2a, 2b), Maroni/Kipendi (3a, 4a, 4b), Maroni East (5), Makere West (6), Makere East (8), Guru East (9), Guru North (10a), Guru South (10b), Mchelelo Research Camp (10c), Mchelelo West (11), Mchelelo East (12), Congolani West (14), Sifa East (16), Sifa West (17), Baomo East (20), Baomo North (21), Mnazini North (26), Kinyadu West (32), Bubesa West 1 (36a), Marembo West (43), Sailoni 2 (47), Kulesa East 1 (48a), Maziwa South (52), Wema West 2 (54), Wema West 3 (55), Hewani South 1 (63), Hewani South 2 (64), Bvumbwe North (65), Bvumbwe South (66), Wema East 4 (68), and Ngumu (72). Map adapted from Mbora [2003].


LEGEND
Study Forest
Forest
TRPNR Boundary
Village
Surface Water
Road
Dike
1°45'
2°00'
2°00'
2°15'
2°15'
Kanjonja
Vukoni
Wenje
Kipende
Maroni
Makere
Baomo
Mukanje
Kitere
Mnazini
Kinyadu
Bubesa
Mwina
Peponi
Sera
Lazima
Marembo
Sailoni
Kulesa
Maziwa
Wema
Bilisa
Hewani
GARSEN
2a
2b
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16
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21
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36a
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47
48a
52
54
55
63
64
65
66
68
72
To Hola
To Malindi
To Malindi
To Lamu
N
0 1 2km
SUDAN
ETHIOPIA
UGANDA
KENYA
SOMALIA
Lake Turkana
Lake Victoria
Mount Kenya
TRPNR
Garsen
TANZANIA
200Km

Zanzibar galago is classified as vulnerable and the Sykes monkey is a regional endemic [Butynski & Mwangi, 1994].

Forest Attribute and Mangabey Abundance Data

Forest attribute and mangabey abundance data were collected within the period August 1998 to November 2001, from 31 forests varying in size from 4.8 to 408 hectares (Fig. 2.1). The forests found throughout the distribution of the mangabey can be classified according to the following characteristics: with or without mangabeys; west or east bank; inside or outside the TRPNR (Table 2.1). An attempt was made to sample each category proportionally. This was not always possible, however, because of location, need for security, extreme current forest clearance, or community opposition. Choice of forests also took into consideration collaboration with a concurrent study on the red colobus [Mbora, 2003].

Table 2.1. Distribution of forests (N) and study forests (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

Forest attribute data also were collected in collaboration with the concurrent study on the red colobus and utilized methods compiled for that study [Mbora, 2003]. Belt transects five meters wide and 100 meters long were randomly established in each study forest [Brower et al., 1998]. They were placed perpendicular to the river in order to sample along the gradient of ground water level, which has been found to be an important determinant of forest species composition and structure [Hughes, 1988]. The transects alternated among being established at the river's edge, the forest's edge, and in the middle of the forest. In those forests less than ten hectares, I sampled three belt transects. This is the minimum needed to reasonably estimate the variance [Zar, 1984]. Additional belts were sampled as forest size increased logarithmically. In forests greater than or equal to ten hectares and less than 100 hectares, I sampled four transects. For those forests greater than or equal to 100 hectares, five transects were sampled. This is preferable to sampling a fixed percentage of the forests because number of species increases with area logarithmically [Haas, 1975; Lomolino et al., 1989].

Within each belt transect, species, height, and DBH of each tree ≥ 10 cm DBH were recorded. Species were identified with the help of Abio Gafo, a local field assistant trained by botanists from the East African Herbarium of National Museums of Kenya. Heights of trees were estimated by sight to the nearest tenth of a meter; DBH was measured with a DBH tape to the nearest tenth of a centimeter. As the mangabeys spend equal amounts of time in the sub-canopy layer and in the canopy layer [Homewood, 1976], measurement of trees ≥ 10 cm DBH sampled both sub-canopy and canopy trees. Three of the top 15 food species for the mangabey (see below) - *Saba comorensis* (Apocynaceae), *Oncoba spinosa* (Flacourtiaceae), and *Polysphaeria multiflora*

(Rubiaceae) – reproduce at sizes less than 10 cm DBH. For these species, individuals less than 10 cm DBH that showed evidence of reproduction (fruits, flowers, or visible remains of these) were recorded. Individuals of *Phoenix reclinata* (Palmae), another of the top 15 food species, can be separated into four size classes [Kinnaird, 1990]. Individuals of size classes 1 (below 1 m in height) and 2 (greater than 1 m in height without obvious trunk) were not recorded, as they did not fit criteria of any forest attribute. Approximately twenty-one percent of reproductive individuals reproduce before the trunk even reaches breast height [Kinnaird, unpub. data, used with permission]; these size class 3 individuals (obvious trunk less than two meters tall) were recorded. The majority of reproductive *Phoenix* is in size class 4 (obvious trunk greater than two meters tall); individuals in this size class were also recorded. In the calculations of basal area (see footnote 1 in Table 2.3) for these four species, an average DBH based on a sub-sample was used (8 cm for *S. comorensis*, *O. spinosa*, and *P. multiflora*; 15.3 cm for *P. reclinata*). Cut stems and branches greater than 10 cm diameter were identified and the diameter was measured where cut. *Phoenix* individuals in size classes 3 and 4 suffering ≥ 50% removal of the fronds or topping of the stem were recorded as harvested. It is only near complete removal of *P. reclinata* fronds (50-100%) and cutting of the trunk that affects reproductive potential (and hence food availability for the mangabeys) [Kinnaird, 1990]. In order to measure area of canopy cover, a black and white photograph was taken of the forest canopy every 20 meters along the transect and continuing to the edge of the forest.

Table 2.2 lists the top 15 food species of the mangabey. The list was generated by averaging percent contributions (to total feeding records) of each species in the diets of six mangabey groups [Homewood, 1976; Kinnaird, 1990; Wieczkowski, in prep. b]. For dioecious species, only half of their basal area was used to calculate the variables ‘basal area of top 15 food species’ and ‘basal area of *P. reclinata*’.

Table 2.2. Top 15 food species of the mangabey, listed in alphabetical order.

Species	Family
Acacia robusta	Mimosaceae
Alangium salviifolium	Alangiaceae
Aporrhiza paniculata	Sapindaceae
Borassus aethiopum (dioecious)	Palmae
Diospyros mespiliformes (dioecious)	Ebenaceae
Ficus natalensis	Moraceae
Ficus sycomorus	Moraceae
Hyphaenae compressa (dioecious)	Palmae
Mimusops fruticosa	Sapotaceae
Oncoba spinosa	Flacourtiaceae
Pachystela msolo	Sapotaceae
Phoenix reclinata (dioecious)	Palmae
Polysphaeria multiflora	Rubiaceae
Saba comorensis	Apocynaceae
Sorindea madagascariensis (dioecious)	Anacardiaceae

Table 2.3 presents a summary of the forest attribute measurements and the calculations performed on them to compute the independent variables used in the multiple regression analyses. Unless otherwise noted, ‘trees’ refers to those with a DBH of 10 cm or greater.

Human forest product use is common in many forests along the lower Tana River, and includes cutting large trees for the construction of canoes and beehives and the

Table 2.3. 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 *Phoenix reclinata* class 4 stems < 50% harvested	- added and divided by number measured	- mean tree height for forest
- trees and *P. reclinata* class 4 stems < 50% harvested	- counted and divided by number of hectares sampled	- density of trees per hectare
- DBH of trees and *P. reclinata* class 4 stems < 50% harvested	- converted to basal area[1], added, and divided by number of hectares sampled	- basal area per hectare
- DBH of individuals (≥ 10 cm DBH) of top 15 food species, *P. reclinata* class 3 & 4 stems < 50% harvested, and reproductive individuals of *Polysphaeria multiflora*, *Oncoba spinosa*, and *Saba comorensis*	- converted to basal area[1], added, and divided by number of hectares sampled	- basal area of the top 15 food species per hectare
- DBH of *P. reclinata* class 3 & 4 stems < 50% harvested	- converted to basal area[1], added, and divided by number of hectares sampled	- basal area of *P. reclinata* per hectare
- DBH of individuals (≥ 10 cm DBH) of *Ficus sycomorus*	- converted to basal area[1], added, and divided by number of hectares sampled	- basal area of *F. sycomorus* per hectare
- DBH of cut trees and *P. reclinata* class 4 stems ≥ 50% harvested	- converted to basal area[1], added, and divided by number of hectares sampled	- basal area of harvested trees per hectare
- DBH of *P. reclinata* class 3 & 4 stems ≥ 50% harvested	- converted to basal area[1], added, and divided by number of hectares sampled	- basal area of harvested *P. reclinata* per hectare

[1] Basal 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.

collection of wild honey, as well as cutting smaller trees for use as building poles. Product use of *P. reclinata* includes cutting of fronds for various uses, and topping the stem for the collection of palm wine or cutting for use as fence poles. Although an extensive level of human forest product use occurred in the years (since 1994) prior to and during data collection [Wieczkowski & Mbora, 1999-2000], any demographic effects in the mangabey population from habitat destruction/alteration might be delayed as a function of prolonged life history factors for these primates [Ovaskainen & Hanski, 2002; see Kinnaird & O'Brien, 1991 for estimates for the Tana mangabey]. I therefore attempted to remove this ‘transient time’ [“the time it takes for a population to return to population-dynamic equilibrium … following a perturbation in the environment,” Ovaskainen & Hanski, 2002, p 285] between forest product use and its effect on the mangabey population by measuring the resources available before recent human forest product use and using those pre-disturbance measures to reanalyze the relationship between the mangabey population and forest attributes. I measured resources available before recent disturbance by combining harvested and non-harvested basal areas into single composite variables. The variables ‘basal area of trees’ and ‘basal area of harvested trees’ were added to form ‘total basal area of trees’. The variables ‘basal area of *P. reclinata*’ and ‘basal area of harvested *P. reclinata*’ were added to form ‘total basal area of *P. reclinata*’. In addition, I corrected the variables ‘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 regression analyses.

The photographs taken of the canopy were scanned into a computer and analyzed for percentage canopy cover using Microsoft PhotoShop. Area of the canopy sampled by the photograph (forest-specific) was calculated with the following equation, solved for Y [Semat & Baumel, 1974]:

$$S'/S = Y'/Y,$$

where S’ = focal length of the camera lens, S = object distance (i.e., mean canopy height for the forest minus the photographer’s height), Y’ = width or length of film, Y = width or length of area of forest canopy. The equation was solved twice, once for width of area of forest canopy (Y_{width}) and once for length of area of forest canopy (Y_{length}). These values were multiplied to get sample area of forest canopy per photograph, which was then multiplied by percent cover of each photograph to calculate area of cover per photograph. These values were added for total area of cover, and divided by total sample area (sample area of canopy per photograph multiplied by the number of photographs taken). This is the independent variable 'area of canopy cover per hectare'.

Forest areas were estimated from 1994 and 1996 aerial photographs of the lower Tana River. These photographs were analyzed using ArcInfo 8.2 and ArcView GIS Version 3.2.

I conducted surveys in each forest in order to sample the average number of mangabey groups using a forest. Because of the mangabeys' ability to travel through some distance of non-forest habitat to visit neighboring forests [Homewood, 1976; Kinnaird, 1990; Wieczkowski, in prep. a], they have access to resources from more than one forest and therefore require fewer resources from a single forest. Consequently, the average number of mangabey groups was deemed a more suitable measure of the mangabey abundance a forest supports than the maximum number of groups ever observed (i.e., during any one survey). An attempt was made to survey each study forest on a monthly basis; this schedule was chosen because preliminary observations on several groups suggested their movement between forests was seasonal (pers. obs.). Forests were searched systematically by traversing the forest along compass directions and transects 100-200 meters apart. Due to the small size of the majority of the study forests, this work was accomplished by a small team moving together. This is a modification of the quadrat census method [National Research Council, 1981], the standard method for censusing Tana primates [Marsh, 1986; Kahumbu & Davies, 1993;

Butynski & Mwangi, 1994]. Surveys were typically undertaken early in the morning (0630-1000 hrs) or late in the afternoon (1400-1700 hrs), times when the mangabeys are most active and vocalizing [Homewood, 1976; Kinnaird, 1990; pers. obs.]. The number of groups seen during all the surveys was divided by the number of surveys undertaken in each forest, for the dependent variable 'mean number of mangabey groups per forest'.

Analysis

One hundred and seven belt transects were sampled in the 31 study forests (mean per forest = 3.45; SE = 0.185; range 2-6). In two forests, I was able to sample only two belt transects: Baomo East (20), because community opposition (to a concurrent World Bank project, and hence to any outsider's presence) prevented us from completing work, and Sailoni 2 (47), because the forest was too small for placement of a third belt.

Three hundred and seventy mangabey surveys were undertaken in the 31 study forests (mean per forest = 11.94; SE = 1.623; range 1-31). Twenty-three forests were surveyed less often than every month. Reasons for this include: the month in which we started working in the forest did not allow for a full year of surveys, the large size of the forest made the risk of underestimating the number of groups (and therefore mangabey abundance) greater than the benefit from surveying every month, and the community's knowledge that mangabeys had been absent for years from the forest. The unequal number of surveys warranted a weighted multiple regression (weighted by the number of surveys in each forest) [Neter et al., 1985].

In order to meet the assumption of a linear relationship between each independent variable and the dependent variable, I transformed certain independent variables [Zar, 1984; Tabachnick & Fidell, 1996]. The variables ‘forest 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*’ underwent square root transformations.

To determine if forest structure, composition, and level of human activity were different between the 15 forests within 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 data were normally distributed) and Mann-Whitney Tests (if data were not normally distributed).

A weighted multiple regression analysis [Neter et al., 1985] was performed on data from the 31 forests to determine if there is dependence between mangabey abundance and the forest attributes. Separate regression analyses were then performed on the two subsets of forests (those within and those outside the TRPNR). The analysis was also conducted with the composite forest attributes (taking into account human use), utilizing data from all 31 forests combined, and then separately for each forest subset. The null hypothesis is that there is no dependence between any of the independent variables (the forest attributes) and the dependent variable (mangabey abundance). The alternative is that at least some of the partial regression coefficients (measure of slope, and hence dependence) are not equal to zero. If the original null hypothesis for multiple regression was rejected, the best fitting regression equation was estimated. All tests were two-tailed.

For those forest attributes found to be important in explaining variation in the mean number of mangabey groups, I also compared values of each attribute between occupied forests and unoccupied forests, using two-tailed Mann-Whitney tests.

RESULTS

There was no significant difference in the mean number of mangabey groups in forests inside the TRPNR and those outside. Three of the 15 (10 original, plus five composite) variables investigated for significant differences between the two subsets of forests differed. Basal area per hectare ($z = -2.411$; $P = 0.016$), basal area of harvested trees per hectare ($t = -2.718$; $P = 0.011$), and total basal area ($t = -3.456$; $P = 0.002$) were significantly smaller within the forests inside the TRPNR than in the forests outside the TRPNR.

The mean number of mangabey groups was positively associated with forest area ($t = 9.086$; $P < 0.0005$) and density of trees ≥ 10 cm DBH ($t = 2.92$; $P = 0.007$) (Table 2.4). The equation for the regression line is Y = -2.043 + 0.280 (square root of forest area) + 0.0025(density of trees). The mean number of mangabey groups within the TRPNR was also positively associated with forest area ($t = 8.552$; $P < 0.0005$) and density of trees ≥ 10 cm DBH ($t = 3.054$; $P = 0.01$) (Table 2.4). The mean number of mangabey groups outside the TRPNR was positively associated only with forest area ($t = 3.19$; $P = 0.007$) (Table 2.4). In each regression model, forest area was responsible for more of the variation in mean number of mangabey groups than the other significant variable (standardized regression coefficients; Table 2.4).

Table 2.4. Standardized regression coefficients for all original independent variables included in the three models. R^2, F-statistic, and sample size also provided for each model.

	All Forests	TRPNR Forests	non-TRPNR Forests
Forest area	0.928**	1.009**	0.649**
Density of trees	0.298**	0.360**	0.111
Mean tree height	0.052	0.106	-0.129
Basal area per hectare	0.103	0.077	0.022
Basal area of top 15 food species per hectare	0.093	0.195	-0.043
Basal area of *Phoenix reclinata* per hectare	0.148	0.159	0.164
Basal area of *Ficus sycomorus* per hectare	0.030	0.068	-0.134
Basal area of harvested trees per hectare	-0.010	0.020	-0.116
Basal area of harvested *P. reclinata*/hectare	-0.012	-0.007	-0.033
Area of canopy cover per hectare	-0.042	-0.024	-0.247
R^2	0.747	0.859	0.421
F-statistic$_{(df)}$	$41.382_{(2,28)}$**	$36.638_{(2,12)}$**	$10.177_{(1,14)}$**
N	31	15	16

*$P < 0.05$
**$P < 0.01$

Analysis incorporating the composite variables indicated that the mean number of mangabey groups in 31 forests was positively associated with forest area ($t = 8.525$; $P < 0.0005$) and total density of trees ≥ 10 cm DBH ($t = 2.284$; $P = 0.03$), consistent with the previous results. The analysis of forests within the TRPNR differed from that utilizing the original variables. While forest area was still significant ($t = 7.627$; $P < 0.0005$), total density of trees ≥ 10 cm DBH was not. In addition, total basal area of the top 15 food species became significant ($t = 2.650$; $P = 0.021$). In both of these models, forest area was still responsible for more of the variation in the response variable than the other significant variable. The mean number of mangabey groups outside the TRPNR was positively associated only with forest area ($t = 3.190$; $P = 0.007$), consistent with the analysis using the original variables. None of the other composite variables was significant.

Finally, mean values of the two independent variables that were significant in the original model, forest area and density of trees ≥ 10 cm DBH were not significantly different between occupied and unoccupied forests. The mean value of total density of trees ≥ 10 cm DBH and total basal area of the top 15 food trees, the significant variables in the model incorporating composite variables, likewise were not significantly different between occupied and unoccupied forests.

DISCUSSION

Analysis of 31 forests throughout the distribution of the Tana mangabey indicated that the only forest attributes that were significantly associated with the mean number of mangabey groups per forest were forest area, which was responsible for most of the variation in mangabey abundance, and density of trees ≥ 10 cm DBH. The relationship between forest area and mangabey abundance was positive, and can be reasoned as follows. Because of the temporally and spatially clumped nature of fruit, species relying on fruit (and seeds) require larger home ranges than folivores in order to obtain adequate food resources [Milton & May, 1976; Clutton-Brock & Harvey, 1977]. The majority of the mangabeys' top diet species have clumped distributions [Kinnaird, 1990; Medley, 1990]. A larger forest should, therefore, provide more area in which the mangabeys can acquire sufficient food from their clumped resources. As the number of species increases with area [MacArthur & Wilson, 1967], a larger forest also should provide more diet species, as well as more individuals of the mangabeys' rarer diet species, several of which are found at low densities [Kinnaird, 1990; Medley, 1990]. In addition, forest edge (and its consequent edge effects) decreases relative to area as forest size increases. Medley [1993b] found a significant positive correlation between mangabey numbers and area-to-perimeter ratio, hypothesized to be because they are a forest-interior species. Edge effects, which can include changes in microclimate, forest structure, tree mortality, and ecological processes, have been measured up to 100 m into the forest interior, substantially reducing the area of forest available to forest species [Saunders et al., 1991; Murcia, 1995; Laurance et al., 1997; Laurance et al., 2002]. Although mangabeys use non-forest habitat as corridors between forests [Homewood, 1976; Kinnaird, 1990; Wieczkowski, in prep. a] and do feed in non-forest habitat [pers. obs.], it is as yet unclear whether they gain any unique advantage from the environmental matrix, as has been suggested for some primates [e.g., see Fimbel, 1994].

Forest area was also significantly associated with mangabey abundance in all other regression models: in forests within the Tana River Primate National Reserve and forests outside the TRPNR when the original variables were analyzed; and in all forests, forests inside, and forests outside when human forest product use was taken into account. This significance of forest area is consistent with Estrada and Coates-Estrada's [1996] finding with *Alouatta palliata* individuals in forest fragments in Los Tuxtlas, Mexico, and Chiarello and de Melo's [2001] surveys of four primates in forest fragments in southeastern Brazil. Similar to the current investigation, these two studies also incorporated fragments of various sizes into their investigations of primate populations in fragmented landscapes.

The relationship between density of trees ≥ 10 cm DBH per hectare and the mean number of mangabey groups was significant and positive in the original regression analysis, for all forests combined and for the subset of forests within the TRPNR. The effect of density was also significant for all forests when accounting for human forest product use (i.e., including harvested trees). Although the mangabey does spend the majority of its time feeding and moving on the ground, tree density is important in that the mangabeys eat food from sub-canopy and canopy trees, and they require canopy trees in which to sleep and to take arboreal refuge from predators.

As there was no significant difference between forests inside and outside the TRPNR in density of trees ≥ 10 cm DBH, this could suggest that it is a difference in the "quality" of the trees present in the different subsets of forests that might be responsible for the lack of significance of this variable in forests outside the TRPNR. Trees inside the TRPNR were not of higher quality in terms of food availability or mean height. Forests inside the TRPNR actually had relatively smaller trees, as evidenced by a significantly lower basal area per hectare despite a similar density compared to forests outside TRPNR. The significance of the density variable in the regression equation for forests inside the TRPNR is therefore not due to an abundance of larger, potentially more productive or supportive trees.

If these measures of habitat "quality" do not differ between the forest subsets, then the difference in significance of density as a predictor of mangabey abundance between forests inside and outside the TRPNR could be hypothesized to result from the increased human activity outside the TRPNR. The measure of basal area of harvested trees per hectare was larger in forests outside the TRPNR, indicative of higher rates of human disturbance in these forests. This variable, however, was tested in the regression analyses and was not a significant predictor of mangabey abundance in any of the models. It may be that the greater human activity outside the TRPNR has a more extensive negative impact on mangabeys than is apparent from analyzing the measured consequences of that activity (i.e., basal area of harvested trees); that is, human presence and activity alone may be influencing mangabey abundance. Wieczkowski and Mbora [1999-2000] reported observations of dogs chasing mangabey groups and ground traps set in forests neighboring farmland. In one forest, I witnessed a group's behavior change markedly (e.g., fewer vocalizations, faster movement, less stationary activity) after it had been chased by dogs. If mangabey groups are avoiding forests with high levels of human presence and activity – those outside the TRPNR more so than those inside – this could mask the positive effect of total density of trees seen for the forests inside the TRPNR.

It does appear that in the forests within the TRPNR, basal area of the mangabeys' top 15 food species is an important predictor, but only when human forest product use is taken into account. Given that many of the mangabeys' important diet species are also ones utilized by humans [Gachugu, 1992; Kinnaird, 1992; Kahumbu, 1992; Medley, 1993a], the original (post-disturbance) variable may have underestimated the food abundance to which mangabey abundance was correlated (due to the possible presence of a 'transient time'). Measures of food availability have also been found to be positively associated with abundance of five cebids across forest types in Brazil [Mendes Pontes, 1999], density of *Procolobus pennantii* in Kibale [Chapman & Chapman, 1999], biomass of frugivorous species in 30 Neotropical sites [Stevenson, 2001], chimpanzee nest density across six sites in Kibale [Balcomb et al., 2000], and densities of *Cebus capucinus*, *Alouatta palliata*, and *Ateles geoffroyi* in Costa Rica [Sorensen & Fedigan, 2000].

The lack of significance of basal area of the top 15 food species in forests outside the TRPNR, despite no significant difference between the two forest subsets in this variable, could be a function of the overriding effect of human activity in those forests, as discussed above. It might also be due to our limited knowledge of the mangabeys' diet, a consequence of spatially limited behavioral observations on the mangabeys. Knowledge of the mangabey's diet comes from observations in only three forests: the Mchelelo Complex (forests number 11, 10c, and 10b), Mnazini North (forest number 26), and Mnazini South (south of Mnazini North) [Homewood, 1976; Kinnaird, 1990; Wieczkowski, in prep. b; Fig. 2.1]. Community similarity indices (percentage of similarity in relative coverage of trees > 20 cm DBH for co-occurring species between two forests) among forests within the TRPNR range from 4.7% to 84% [Medley, 1990]. Lists of diet species are likely to vary across the mangabey's distribution because of this variation in species composition, potentially limiting the strength of the current list to measure food abundance distribution-wide. This is similar to the finding by Onderdonk and Chapman [2000], who reported that the number of food trees in various forest fragments did not significantly explain variation in presence/absence of three primates. In their study, the measure of food abundance was based on diet data from primate populations inside Kibale National Park, Uganda, while the presence/absence data were collected in fragments outside the park, where tree species composition and diet potentially differed.

Occupied and unoccupied forests did not differ in the mean value of any of the significant variables: forest area, density of trees, total density of trees, or total basal area of top 15 food trees. The reasons for mangabey absence in the unoccupied forests must, therefore, be looked for elsewhere. Mangabeys have not been sighted in forests 3b, 4a, 4b, or 6 in any of the censuses undertaken since 1972/74 [Butynski & Mwangi, 1994]. One very likely possibility for their absence is the proximity of these forests to human habitation and farmland (Fig. 2.1), which may also be affecting forests 32 and 36a. As discussed above, Wieczkowski and Mbora [1999-2000] observed mangabeys raiding crops, traps set for crop raiders, and mangabeys being chased by dogs in other occupied forests close to farms. Another factor contributing to the absence of mangabeys could be the distance of the unoccupied forests from neighboring occupied forests. The last census to observe mangabeys in forest 36a was the 1975 census [Marsh, 1978]. Mangabeys were not seen in 1989 [Kinnaird & O'Brien, 1991] or 1994 [Butynski & Mwangi, 1994]. Even if conditions in that forest can now support mangabeys, the animals may not be able to travel to it from the distant neighboring forests. Forest 36a is approximately 1.5 km from the nearest occupied forest, a longer distance than the maximum distance (1 km) of non-forest habitat mangabeys have been observed moving through [pers. obs.]. Finally, these unoccupied forests may differ from occupied forests in some un-measured ecological attribute that affects mangabey distribution and/or movement. Although comparisons over short (15 km) distances are advantageous because un-measured ecological attributes are less likely to differ [Chapman & Chapman, 1999], such variables as seasonally important food species and levels of competition could differ over the longer (60 km) extent of the mangabey's distribution.

In the most recent IUCN/SSC action plan for African primates, Oates [1996] recommends that a long-term management plan be written for the Tana River forests, including consideration of translocating monkeys from unprotected forests outside the TRPNR to protected and unpopulated forests within the TRPNR. The research presented here, particularly the potential for the regression equation to predict the mean number of mangabey groups in forests not sampled for this study, could serve as one aspect of an evaluation of translocation as a conservation measure for the Tana mangabey. That is, forests with fewer groups than predicted might be considered candidates for receiving translocated groups. Translocation, or "the deliberate movement of wild primates from one natural habitat to another for the purpose of conservation or management" [IUCN/SSC, 2002, p 33], has been attempted for certain primates [e.g., *Alouatta*: Crockett, 1998; Ostro et al., 1999; *Leontopithecus rosalia*: Kierulff et al., 2002; *Papio anubis*: Strum, 2002], and has been recommended in both specific cases [e.g., *Cercopithecus neglectus*: Mugambi et al., 1997; *Alouatta*: Crockett, 1998; Horwich, 1998; *Hylobates moloch*: Andayani et al., 2001] and in general [Konstant & Mittermeier, 1982**;** Caldecott & Kavanagh, 1983; Strum & Southwick, 1986; IUCN/SSC, 2002]. Before translocation, re-introduction, or rescue can be considered as conservation tools, however, the protection of the release habitat from destruction and of the released animals from hunting must be assured [Konstant & Mittermeier, 1982; Caldecott & Kavanagh, 1983; Boinski & Sirot, 1997; Crockett, 1998; Horwich, 1998; Richard-Hansen et al., 2000; González-Solís et al., 2001; Gadsby, 2002; Horwich et al., 2002; IUCN/SSC, 2002; Kierulff, et al., 2002]. This is not the case currently in Tana River, where the forests are still being cleared and forest product use remains common, including within the TRPNR. Protection and management of the forests would benefit the primates more at this point than any consideration of translocation.

In order to best manage the Tana River forests for the mangabey, management should focus on those forest attributes that were significantly correlated with variation in mean number of groups per forest, 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; those restoration activities recommended and 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]. For example, instead of cutting *F. sycomorus* for dugout canoes, a species that is easy to carve but lasts only one year, use of *Mimusops fruticosa* should be encouraged. *Mimusops* is more difficult to carve, but lasts eight years [Kahumbu, 1992]; it is also less utilized by the mangabeys [Homewood, 1976; Kinnaird, 1990]. Likewise, *Hyphaenae compressa*, a very numerous palm, could be used for beehives instead of the less numerous *F. sycomorus*. Beyond this, research should be expanded to study diet of groups living in other areas of the mangabey's distribution, especially in the south where species composition of the forests differs (Medley, 1992), which would provide spatially-specific lists of important diet species. This information will contribute to management planning for both forest restoration and restriction of human forest product use.

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CHAPTER 3

TEMPORAL COMPARISONS OF BEHAVIOR AND DIET IN A TANA MANGABEY (*Cercocebus galeritus*) GROUP[1]

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ABSTRACT

The behavior and diet of a group of Tana mangabeys (*Cercocebus galeritus*) was studied, continuing the long-term investigation of this species. Data collection was consistent with earlier studies of this group in 1974 and 1988-89, allowing for a number of behavioral, dietary, and ecological comparisons among the three studies. Behavioral and dietary data were collected utilizing scan samples during monthly 3-day follows of the group over 12 months. Density and phenological data for the mangabey's most important diet species were also collected throughout the group's home range. The group in 2000-01 was similar to the group in 1988-89 in several measures, including increased rates of eating, foraging, and moving, as well as consuming less fruit and more seeds, relative to the group in 1974. One significant difference between the groups in 1988-89 and 2000-01 was an overall increase in consumption of ripe seed. The assumption that the mangabey consumes ripe fruit in correlation to availability was not supported by analysis of seven species combined in 2000-01. When the seven species were analyzed individually, however, the group in 2000-01 consumed ripe fruit, ripe seed, unripe fruit, and/or unripe seed in correlation to availability. Ecological explanations for the dietary differences among the three groups are limited. Observed changes in the activity budget of the group in 2000-01 appear to be related to the group's increased size and diet differences. This study increases our understanding of the ecological flexibility of the mangabey, information critical to successful management and conservation.

KEY WORDS: *Cercocebus galeritus*; temporal comparison; diet; ecological flexibility

INTRODUCTION

Seasonal changes in primate reproductive behavior (e.g., Vandenbergh and Vessey, 1968; Butynski, 1988; Fernandez-Duque *et al.*, 2002), diet (e.g., Terborgh, 1983; Dasilva, 1994; Brugiere *et al.*, 2002), ranging (e.g., Clutton-Brock, 1975; Terborgh, 1983; Mitani, 1989; Kaplin, 2001), and activity budgets (e.g., Marsh, 1981; Lawes and Piper, 1992; Doran, 1997) have long been recognized and investigated. These changes are often correlated with seasonal changes in habitat productivity (e.g., Terborgh, 1983; Dasilva, 1994; Kaplin, 2001), but have also been found to be correlated with rainfall/water availability (e.g., Altmann and Altmann, 1970; Butynski, 1988), and temperature and photoperiod (e.g., Lawes and Piper, 1992; Fernandez-Duque *et al.*, 2002). Such data are important in the general investigation of how primates respond to their environments, as well as in addressing questions related to the potential for interspecific competition (Chapman, 1987) and possible constraints on primate numbers or biomass (Fleury and Gautier-Hion, 1999; Brugiere *et al.*, 2002).

As multi-year studies become more common, data accumulate that allow investigation of the ecology and behavior of primates over longer temporal scales (Goodall, 1983; Hamilton, 1985; van Schaik and van Noordwijk, 1985; Chapman, 1987; Crockett and Rudran, 1987; Norton *et al.*, 1987; Olupot, 1988; Olupot *et al.*, 1994; Gould *et al.*, 1999; Okamoto *et al.*, 2000; Chapman *et al.*, 2002; Jolly *et al.*, 2002). These long-term studies, whether longitudinal or intermittent, can also expand our knowledge of the behavioral and ecological flexibility of primates. For example, *Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus* have been observed to eat certain diet species in only one of the two or three years of observation of those primates in Costa Rica (Chapman, 1987); without the additional one or two years of data, those diet species would not have been recognized as important. A similar conclusion was reached by Norton *et al.* (1987) in a five-year study of the diet of *Papio cynocephalus* in Mikumi National Park, Tanzania. Long-term studies also permit evaluation of the effects of environmental perturbations that occur infrequently or on expanded temporal scales. For example, Gould *et al.* (1999), only by collecting ten years worth of demographic data, were able to conclude that *Lemur catta* populations were capable of recovering quickly after a natural disaster (in this case a drought) caused their population to decline. Similarly, skewed adult sex ratios in a population of *Papio ursinus* were readily explained with data collected during a severe food and water shortage which had occurred five to seven years earlier (Hamilton, 1985).

Information on interannual differences in reproduction, behavior, and ecology will also prove critical in conservation work. It is only with long-term data that we know the life history parameters of endangered species, which can then be used in population viability analysis (Okamoto *et al.*, 2000). In addition, interannual changes in habitat attributes (e.g., in phenology, density of trees, or forest area) can be linked with changes in primate ecology between the same years to understand how species respond to the contemporary large-scale habitat changes that are of significant concern (Johns, 1986; Decker, 1989; Kinnaird, 1990; Olupot, 1998). The greater our understanding of the resource needs and flexibilities of primates, the better we can plan management actions (Chapman *et al.*, 2002).

The Tana River in Kenya is a meandering and flooding river that creates a dynamic and changing environment for the primates and other fauna that depend upon its riverine forests. The creation of ox-bow lakes and new river channels, the periodic flooding of the forests, and changes in the level of the water table under the forests lead to a mosaic of heterogeneous and variable forest patches along the lower Tana River (Hughes, 1988, 1990). The forests also exhibit interannual variation in production of leaf buds, new leaves, flowers, and fruit (Marsh, 1978b; Kinnaird, 1992). This dynamic ecosystem is therefore an ideal place in which to study temporal variability, both in terms of environmental parameters and the correlated ecological and behavioral changes in the animals residing in this biogeographic area.

The lower Tana River has been the site of a number of studies over the past three decades. Although none of these have been continuous, several studies have documented long-term changes in the forests and the resident primates (Marsh, 1986; Decker, 1989; Kinnaird, 1990; Medley, 1990; Wieczkowski, in prep. b). The Tana mangabey (*Cercocebus galeritus*) has been the subject of two of these studies (Homewood, 1976; Kinnaird, 1990), in addition to the current study. Homewood (1976) focused on two mangabey groups in different forests, one with a very high mangabey density and the other with an intermediate density, in order to learn how mangabeys shift their "patterns of exploitation" in response to seasonal and local differences in their habitat. She found a significant amount of flexibility on the part of the mangabeys, evident in their diet, ranging, and intergroup interactions, which allowed them to survive in the temporally and spatially fluctuating environment.

Kinnaird (1990) compared Homewood's data from fourteen years prior to her own to study how diet and behavior in the same mangabey groups had changed. She found that the mangabey groups in 1988-89 fed on greater amounts of unripe and ripe seeds than they did in 1974. This change in diet items between the studies was hypothesized to be a result of loss of important food trees in either one or both of the study forests (resulting from forest loss and fragmentation due to river changes and extensive clearance of forest for agricultural land), or increased competition with Tana baboons (*Papio c. cynocephalus*). The observed increase in time spent feeding was then attributed to the lower quality diet (i.e., the higher proportion of seeds, as compared to ripe fruits eaten by the groups in 1974).

The current study was undertaken to extend the previous temporal comparison to include another decade worth of change in the habitat and ecology of the mangabeys. Data were collected on one of the mangabey groups that was also studied by Homewood (1976) and Kinnaird (1990). In this article, I investigate changes in behavior and diet of this group, and attempt to link those changes to changes in the habitat, particularly food abundance. Because seasonal changes play a role in primate ecology, I also re-evaluated Kinnaird's (1990) general conclusions from comparisons between her 15-month data and Homewood's (1976) 7-month data, by limiting Kinnaird's dataset to the same months as Homewood's and comparing on that basis.

The current study also permitted evaluation of Kinnaird's (1990) hypothesis that she proposed to explain the dietary changes observed between the group in 1988-89 and the group in 1974. Although direct testing of this hypothesized decline in ripe fruit availability and an associated switch to consumption of unripe seeds is not possible due to limitations of the data presented by Homewood (1976) and Kinnaird (1990), data collected in the three studies did permit evaluation of changes in fruit abundance between them. In addition, the additional data collected on the group in 2000-01 provided the opportunity to examine the dietary preference by the mangabey for ripe fruit (an assumption of the hypothesis), as well as testing an important corollary of Kinnaird's hypothesis: that the mangabeys consume ripe fruit in accordance with its availability (a positive correlation) and they "compensate" for declines in ripe fruit availability by consuming alternative diet items (e.g., unripe seeds) in relation to that decline (a negative correlation).

The *Cercocebus* clade is characterized by dental morphology adapted for eating hard nuts and seeds (Fleagle and McGraw, 2002), and all *Cercocebus* species include seeds in their diet (*C. torquatus*: Mitani, 1989; *C. agilis*: N. Shah, pers. comm.; *C. atys*: Rutte, 1998 in Fleagle and McGraw, 2002; *C. galeritus*: Homewood, 1976; Kinnaird, 1990). These observations also supported an alternative hypothesis that rather than concentrating their diet on ripe fruit and compensating for changes in fruit availability by consuming less-preferred items, the Tana mangabeys are instead consuming their various dietary items (e.g., ripe fruit and seed, unripe fruit and seed) in positive correlation with availability of each item. This more inclusive hypothesis was also tested utilizing dietary data for the group in 2000-01.

The intent of this study is to further examine the extent and nature of the apparent ecological flexibility of the Tana mangabey. Given that this primate is one of the most endangered of all primates (Mittermeier and Konstant, 2002), our ability to gauge its response to naturally-occurring as well as anthropogenic changes in the Tana River ecosystem will be valuable in conservation planning and effective management of the area supporting its threatened population.

METHODS

Study Area and Group

The study was undertaken within the Tana River Primate National Reserve (TRPNR) in southeastern Kenya (Fig. 3.1). The forests within the Reserve are not dependent on rainfall within the lower Tana River area. With a mean annual precipitation of only 582 mm (averaged by month for 38 months 1996-2001; unpublished climatological data, Mchelelo Research Camp), the area is considered arid/semi-arid. The forests are therefore riverine forests, dependent on the Tana River's processes of inundation, sediment transport, erosion, and alluvial deposition, and the height of the groundwater table (Medley, 1990). Rainfall in the lower Tana occurs in two rainy seasons: the short rains of November and December, and the long rains of March through June. The mean daily minimum temperature is 23.1°C and the mean daily maximum temperature is 32.9°C; the coldest months are June and July, while the warmest months are January-March (unpublished climatological data, Mchelelo Research Camp).

The 169 km^2 TRPNR, gazetted in 1976 to protect populations of the Tana mangabey and the Tana River red colobus (*Procolobus rufomitratus*), as well as their riverine forest habitat, is positioned in the northern 30 kilometers of the primates' 60-kilometer distribution. Both of the primate species were recently included in the list of the "Top 25 Endangered Primates" (Mittermeier and Konstant, 2002), are listed as "Critically Endangered" (IUCN, 2000), and are CITES Appendix I taxa (IUCN, 1996). The TRPNR also provides habitat for six other non-human primate species: Sykes monkey (*Cercopithecus mitis albotorquatus*; a regional endemic), vervet monkey (*Cercopithecus aethiops pygerythrus*), yellow baboon (*Papio c. cynocephalus*), Zanzibar

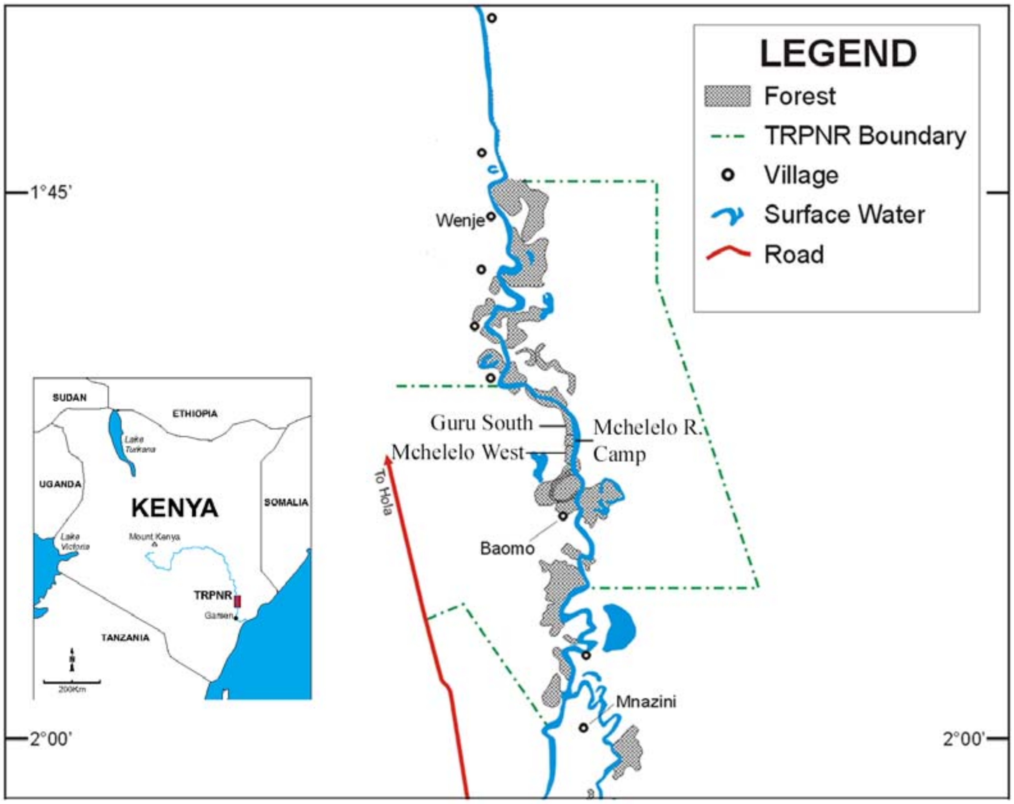

Fig. 3.1. The Tana River Primate National Reserve (TRPNR), with study forests named. Adapted from Mbora (2003).

galago (*Galago zanzibaricus*, vulnerable), Senegal galago (*Galago senegalensis*), and Garnett's galago (*Otolemur garnettii*) (Andrews *et al.*, 1975; Butynski and Mwangi, 1994).

The study group, referred to here as the Mchelelo West group, had a mean size of 50 mangabeys and ranged in Guru South forest, Mchelelo Research Camp, and Mchelelo West forest during the 2000-01 period of study (Fig. 3.1). This is one of the groups studied by Kinnaird in 1988-89 (1990) and Homewood in 1974 (1976). The group was larger in 2000-01 than in either 1988-89 (17 individuals) or in 1974 (36 individuals). The group in 2000-01 was also larger than the mean size of 17 groups counted in 1999-2001 (30.4, range 6-62, SE = 3.37; Wieczkowski and Mbora, 2002).

Group Size and Composition Data and Analysis

An attempt was made during each 3-day sample (see below) to obtain a complete group count of the study group; counts were considered complete based on the quality of view of the group and general agreement with previous and subsequent counts. Age-sex composition was also recorded, following the categories in Homewood (1976). Mean group counts are also available from Homewood (1976) and Kinnaird (1990). χ-Square Tests of Independence were conducted to determine if age-sex composition significantly changed across the three studies.

Behavioral Data Collection

Data were collected on the group from 0700 to 1815 hours in one block of three days (3-day sample) per month from August 2000 until July 2001 (Homewood, 1976;

Kinnaird, 1990). Every half hour, ten minutes were spent taking a scan sample (Altmann, 1974) of the group, recording for each visible individual the first behavior sustained for five seconds, and if eating or foraging, the species, food item, and stage of ripeness. Behavioral categories recorded were ‘eat’, ‘forage’, ‘move’, ‘social/sexual’, ‘inactive’, and ‘other’, and follow those used by Homewood (1976) and Kinnaird (1990). ‘Eat’ was defined as an animal chewing or ingesting a food item, either directly from the habitat or from its cheek pouches; animals drinking or nursing were also scored as eating. Animals eating while engaging in any other activity were scored as eating. ‘Forage’ was defined as an animal searching for (examining leaf litter, tree trunks, or foliage with the hands or eyes), manipulating, or preparing a potential food item. ‘Move’ was defined as any horizontal or vertical locomotion; movement as a consequence of other activities, for example ‘forage’ and ‘social/sexual’, was not scored as ‘move’. ‘Social/sexual’ was defined as an animal involved with at least one other animal in one of a variety of activities: allogroom, sexual, play, and agonistic. Because of the inherent social nature of vocalizations, any animal vocalizing (e.g., adult male ‘whoop gobble’, contact calls, shrieks and grunts in agonistic encounters) was scored as ‘social/sexual’. ‘Inactive’ was defined as an animal being stationary and not engaged in any other recorded behavioral activity.

Homewood (1976) collected data for seven months, from February until August 1974. Kinnaird (1990) collected 15 months of data from January 1988 until March 1989. Because of the need to sample from the same months to control for seasonal changes, sub-samples from the current study (Feb-Jul 2001 and Aug 2000) and that of Kinnaird (Feb-Aug 1988) were taken to correspond to Homewood’s seven months. These form the basis for comparisons across all three studies. Comparisons incorporating a full yearly cycle were possible between this study (data collected from Aug 2000-Jul 2001) and Kinnaird's (using data from Feb 1988-Jan 1989). All comparisons are with data presented in Homewood (1976) and Kinnaird (1990), except where specifically noted.

Behavioral and Dietary Data Analysis

To estimate the percent time spent in each of the six recorded behavioral categories, I divided the number of records of each behavior by the total number of records each day of observation and multiplied by 100. For purposes of comparison, Homewood's and Kinnaird's behavior 'allogroom' was added to the behavioral category 'social/sexual'. Values for each day of observation in Kinnaird's study were calculated from the means and standard errors published in her dissertation (1990).

The percent contribution of each diet item (i.e., fruit, seed, etc.) was calculated for each 3-day sample. Analysis of diet items across all three studies was limited to a comparison by major type (i.e., fruit, seed, stem/new growth, leaf, animal) because Homewood (1976) did not distinguish between ripe and unripe material in the Mchelelo West group's diet. Kinnaird did distinguish between ripe and unripe material and comparisons with her data were expanded to include differentiated ripe and unripe fruit and seeds. Mangabeys were scored as eating seeds when they discarded the valve (for *A. robusta*), removed the peel and pulp (e.g., *P. reclinata*, *D. mespiliformes*), or bit off chunks of the fruit to consume the liquid endosperm (for *H. compressa*). "Dry" seeds with no remaining pulp that were picked from the ground (e.g., *P. reclinata*, *A. robusta*, *S. madagascariensis*) were scored as ripe seeds.

Descriptive statistics presented for the 2000-01 behavioral data include means ± standard errors based on 21 (seven months) or 36 (twelve months) daily values. Daily values were calculated from each day's observations; the mean number of behavioral records collected per day was 296 and 271 during seven months and twelve months, respectively. In total, I collected 6216 behavioral records during the seven-month period and 9759 during the twelve-month period. Daily values were used in the statistical tests of the behavioral data. Descriptive statistics for the 2000-01 diet data include means ± standard errors that were calculated from monthly values ($n = 7$ or $n = 12$). These monthly values were used in all statistical tests of the diet data.

All statistical tests performed on the behavioral and diet data were two-tailed. Statistical comparisons among all three studies utilized analyses of variance (ANOVAs), with least significant difference (LSD) post hoc multiple pairwise comparisons, if the data were normally distributed. A Two-Way ANOVA was performed on the behavioral data, with study and month entered as the main effects. The main interest is in the effect study has on mean percent time spent in each behavior; month was not of interest but was added as a blocking factor. A One-Way ANOVA was performed on the diet item data with study as a fixed factor. If the data were not normally distributed, the Friedman Test was applied, with the Wilcoxon Signed-Ranks Test used to test pairwise differences. The 12-month comparisons between Kinnaird (1990) and the current study were based on Paired-Samples *t* Tests if the data were normally distributed, and Wilcoxon tests if they were not.

Ecological Comparisons

Ecological comparisons were also made across the three study periods in order to contextualize and evaluate changes or similarities in behavior and diet. All statistical tests performed were two-tailed.

Density comparisons. In order to determine if density of important mangabey diet species had changed between studies, reproductive-sized individuals of 25 species were enumerated throughout 39.5 hectares of the group's range in 2000-01 and the entire forested range (16.25 ha) of the group in 1988-89 (Kinnaird, 1990). A density was then calculated for each species.

Data are not available from Homewood (1976) to enable comparisons of density of food species with that study. Comparisons can be made, however, in 9 hectares of Mchelelo West forest between 1975 (Marsh, 1978a) and 1988 (Decker, 1989). Although this is not the full range of either group in 1974 or 1988-89, it will serve as a general comparison of forest composition between those time periods. Comparisons were made with Wilcoxon Signed Ranks Tests.

Phenological data collection in 2000-01. For the purpose of investigating if differences in fruit availability are related to behavioral and dietary differences exhibited by the group, phenological data were collected for comparison with the earlier studies. In the three forests used by the mangabey group during the current study, 226 individual trees from 11 species were monitored for phenological activity on the day immediately prior to or subsequent to each 3-day sample. A list of the top 15 diet species was created by averaging the percent contributions of each diet species (fungi and grass excluded) across the five mangabey groups previously studied (Homewood, 1976; Kinnaird, 1990).

These averages were then ranked and the top 15 species determined. Homewood (1976) found that percent contribution to the diet was significantly correlated to canopy abundance for the top 20 food species eaten by the mangabey groups she studied. I therefore determined the abundance (see Wieczkowski, in prep. a, for methods of determining abundance) of each of the top 15 diet species in each of the forests, and selected the nine most abundant. The nine most important food species in the diets of the mangabey groups studied previously range from 69% to 92.8% of the annual diet (Homewood, 1976; Kinnaird, 1990). Nine species, therefore, appeared to be an adequate sample to test for the relationship between food abundance, diet, and behavior. Because of the absence of a number of plant species in Mchelelo Research Camp, only six species were monitored there. For most species, ten individuals were monitored; for species whose populations did not include ten individuals, all individuals present in the forest were monitored. The presence of unripe and ripe fruit was scored separately on a 0-5 scale measuring the proportion of the total canopy covered by fruit (0 = 0%, 1 = 1-20%, 2 = 21-40%, 3 = 41-60%, 4 = 61-80%, 5 = 81-100%) (Homewood, 1976). Each tree's diameter at breast height (DBH) was also measured, and a mean for each species was calculated. Each mean monthly fruit score was multiplied by the species-specific mean DBH and density values (mean monthly fruit score x species density x species mean DBH). This was done to better estimate biomass of available fruit per hectare, as density of trees can influence fruit availability habitat-wide (Harrison, 1984; Chapman *et al.*, 1994) and DBH is considered an accurate estimate of crown volume (Phillips, 1995) or fruit number and/or biomass (McDiarmid *et al.*, 1977; Leighton and Leighton, 1982; Chapman *et al.*, 1992).

Phenological comparisons between 1974 and 2000-01. Homewood (1976) had collected phenology data on five species in common with the current study. Her sample sizes, however, were three or five individuals per species. Because there are no density or biomass data that can strengthen a comparison with her limited data, phenological comparisons between Homewood's (1976) study and the current study could not be undertaken.

Phenological comparisons between 1974 and 1988-89. Although densities of food species are not available for comparison between 1974 and 2000-01, they are available to undertake a comparison between 1974 and 1988-89. I was therefore able to combine phenology and density into one measure of food availability; Kinnaird (1990) had used these datasets individually. Fruit availability for six species could be compared between the two studies: *Phoenix reclinata*, *Acacia robusta*, *Hyphaenae compressa*, *Diospyros mespiliformes*, *Ficus sycomorus*, and *F. natalensis*. Using raw phenology scores from Kinnaird's unpublished data (access granted by M. Kinnaird), I first changed fruit scores (on the 0-5 scale) for individual trees to a percent by taking the mid-point of the score on the percentage scale (see above) (0 = 0%, 1 = 10%, 2 = 30%, 3 = 50%, 4 = 70%, 5 = 90%) (Homewood, 1976). I then summed these percentages by species within each month, and divided them by the number of trees sampled. Densities from 1975 and 1988 were obtained from data collected by Marsh (1978a) and Decker (1989), respectively, for all but the two palms (*H. compressa* and *P. reclinata*). For each of the four species with density data, the density in 1975 was multiplied by each month's fruit score from Homewood (1976), and the density in 1988 was multiplied by each month's fruit score from Kinnaird. Estimates of fruit availability (composite values for four species, mean monthly fruit scores for two palms) for the six species were lumped by study and compared with a Wilcoxon Test.

Phenological comparisons between 1988-89 and 2000-01. For the phenological comparisons between 1988-89 and 2000-01, I estimated fruit biomass with a composite value of mean monthly fruit score, species density, and species DBH (mean monthly fruit score x species density x species mean DBH). Kinnaird measured the DBH of each tree in her phenology sample; access to these unpublished data was also granted. Values for seven species (*P. reclinata*, *A. robusta*, *H. compressa*, *Oncoba spinosa*, *D. mespiliformes*, *Sorindea madagascariensis*, and *F. sycomorus*) were lumped by study and compared with a Wilcoxon Signed Ranks Test. The comparison was then undertaken separately with unripe fruit biomass scores and ripe fruit biomass scores.

Correlations Between Diet Item Availability and Consumption

To evaluate Kinnaird's (1990) hypothesis that dietary changes in the mangabey are due to changes in ripe fruit availability, one-tailed Spearman's correlations were used to test for a positive correlation between ripe fruit availability and consumption, and for negative correlations between ripe fruit availability and consumption of ripe seed, unripe fruit, or unripe seed in 2000-01. The analysis included monthly biomass scores for ripe fruit in seven species (*P. reclinata*, *A. robusta*, *H. compressa*, *O. spinosa*, *D. mespiliformes*, *S. madagascariensis*, and *F. sycomorus*) and monthly percent consumption of each diet item eaten.

I also investigated if the mangabeys consume any diet item (i.e., ripe fruit, ripe seed, unripe fruit, and unripe seed) in positive correlation with availability (ripe fruit and unripe fruit) in 2000-01. The analysis was expanded to also examine correlations in the seven species individually, based on calculation of the percent contribution to the diet of each species item (e.g., *A. robusta* ripe seed, *S. madagascariensis* unripe fruit) eaten during each 3-day sample. Correlations were determined by one-tailed Spearman's correlations.

RESULTS

Group Size and Composition

The mean size of the mangabey group in 2000-01 was 50 individuals (n = 23 complete counts). This group was larger than either the group in 1988-89 or in 1974 (Table 3.1). The actual rate of increase (r, in individuals per individual per year) between 1974 and 1988 was -.05, the rate between 1974 and 2000-01 was 0.01, and the rate between 1988-89 and 2000-01 was .09. The increase over the group in 1974 came in the subadult male, adult and subadult female, juvenile, and infant categories. Only the adult male category saw a decrease, by one individual. The increase over the group in 1988-89 came in all categories, but most importantly in the immature age categories (subadult, juvenile, and infant), indicative of an expanding population. The adult and subadult male:female ratio was 1:2.1 in 2000-01, 1:6 in 1988-89, and 1:2 in 1974. There was no significant change in this ratio among the three studies. The adult female to immature ratio was 1:2.4 in 2000-01 and 1:1.7 in 1988-89, also a non-significant change.

Table 3.1. Mean group composition of the Mchelelo West mangabey group during the three studies.

Study	AM	SM	AF	SF	J	I	Total
2000-01[1]	3	7	14	7	13	6	50
1988-89[2]	1	0	6	0	8	2	17
1974[3]	4	4	16		8	4	36

[1] this study; [2] Kinnaird (1990); [3] Homewood (1976), who did not distinguish between adult and subadult females
AM=adult males; SM=subadult males; AF=adult females; SF=subadult females; J=juveniles; I=infants.

next most common behaviors were forage (16.6 ± 1.0%), move (13.6 ± 0.9%), social/sexual (8 ± 0.7%), and inactive (8.7 ± 0.5%). These values for mean percent time spent in the five behaviors were similar to the values when annual means (August 2000 to July 2001) were calculated: eat 50.1 ± 1.4%; forage 15.3 ± 1.1%; move 14.5 ± 0.8%; social/sexual 8.6 ± 0.6%; and inactive 9.9 ± 0.8% (Fig. 3.2).

Significant differences in mean percent time eating and foraging were seen among the three studies (Fig. 3.2; Table 3.2). Time spent eating and time spent foraging were significantly higher in both 1988-89 and 2000-01 than in 1974; there were no significant differences in these behaviors between 1988-89 and 2000-01. There was no difference in mean percent time spent in social/sexual activities among the studies (Fig. 3.2; Table 3.2). A significant decrease was found between 1988-89 and 2000-01, however, when the comparison was expanded to twelve months of data (Fig. 3.2; Table 3.2).

There are differences among the three studies in mean percent time spent in the two remaining behaviors, move and inactive (Fig. 3.2; Table 3.2). The group spent significantly less time in these behaviors in 1988-89 and 2000-01 than it had in 1974. In

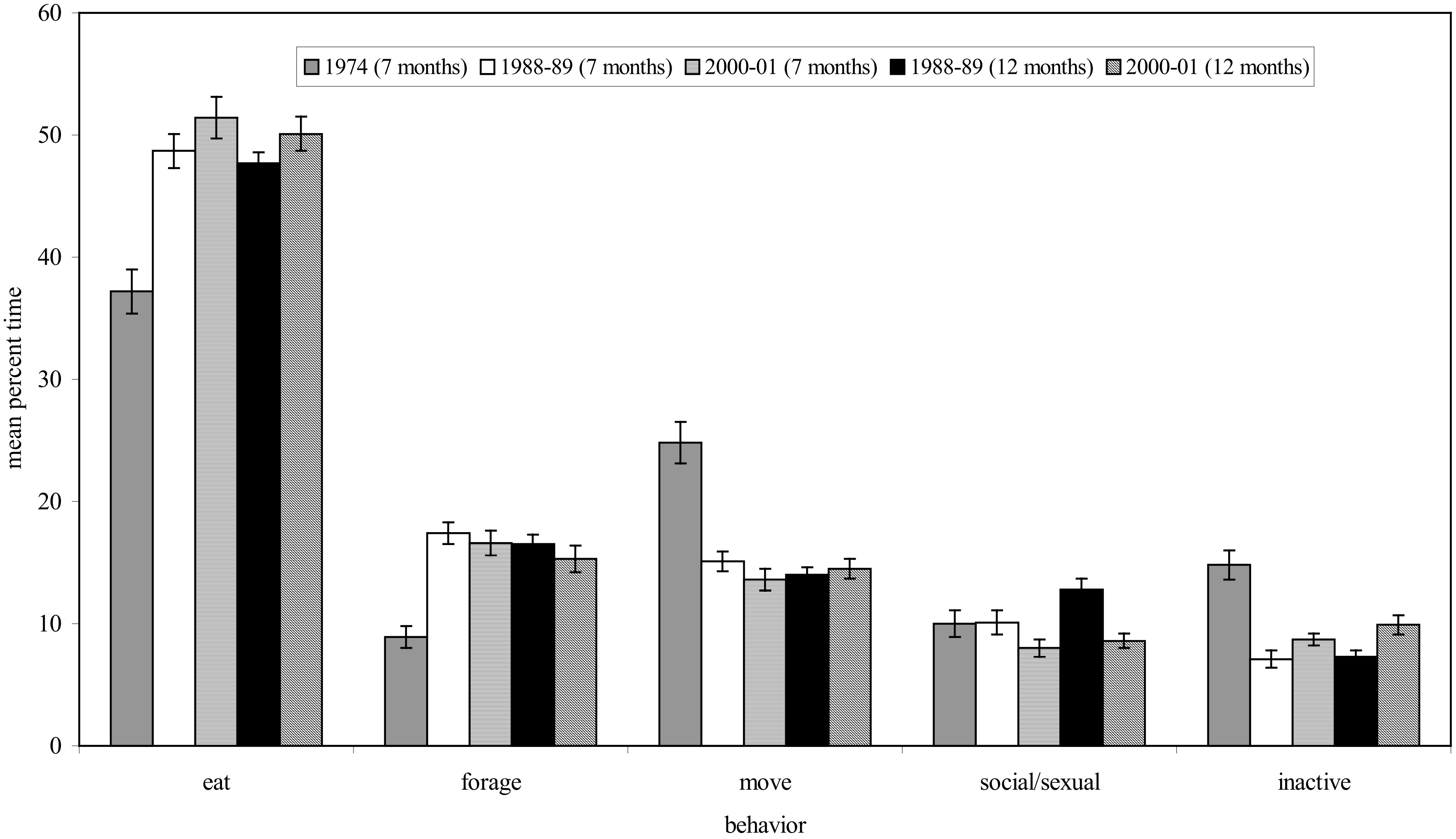

Fig. 3.2. Mean percent time the groups in 1974, 1988-89, and 2000-01 spent in each of five behaviors. Error bars display plus or minus one standard error from the mean.

Table 3.2. Results of statistical tests comparing mean percent time spent in five behaviors among three studies, and between two studies (based on a full 12 months of data). Significant differences were found with post hoc least square differences comparisons or Wilcoxon Signed-Ranks Tests ($p < 0.05$).

	1974 vs. 1988-89 vs. 2000-01			1988-89 vs. 2000-01		
Behavior	F / χ^2	p	Significant differences	t	p	Significant difference
Eat[a]	39.158	0.0005	2000 & 1988 > 1974	-1.777	0.084	no difference
Forage[a]	47.829	0.0005	2000 & 1988 > 1974	0.914	0.367	no difference
Social/sexual[a]	1.649	0.204	no differences	3.373	0.002	1988 > 2000
Move[b]	17.238	0.0005	2000 & 1988 < 1974	-0.542	0.591	no difference
Inactive[b]	14.857	0.001	2000 & 1988 < 1974	-3.27	0.002	1988 < 2000

[a] analyzed with Two-Way ANOVA (*F*); df = 2

[b] analyzed with Friedman Test (χ^2); df = 2

df for *t* Test = 35

the full 12-month comparison, the mangabeys spent more time being inactive in 2000-01 than in 1988-89 (Fig. 3.2; Table 3.2).

Diet Items

The seven-month diet of the mangabey group in 2000-01 consisted primarily of seeds (49.2 ± 3.7%) (Fig. 3.3). The diet also consisted of 23.1 ± 4.4% fruit, 11.3 ± 1.5% animal matter, 8.8 ± 2.4% stem/new growth, and 4.7 ± 1.4% leaf. The group's annual diet consisted of 27.5 ± 4.9% ripe seed, 19.8 ± 4.8% ripe fruit, 19 ± 4.4% unripe seed, 10.9 ± 1.1% animal matter, 7.6 ± 1.6% stem/new growth, 5.8 ± 1.6% unripe fruit, and 3.8 ± 0.9% leaf (Fig. 3.4). Overall, the annual diet consisted primarily of seeds (46.5 ± 3.6%) and fruit (25.6 ± 4.4%). Ripe materials made up 47.3 ± 5.0% of the diet, with the majority of those being ripe seeds. Unripe materials made up 24.8 ± 4.4% of the diet, with the majority being unripe seeds. Animal matter included insects and snails.

The mangabeys ate significantly less fruit and more seed in 2000-01 and in 1988-89 than they did in 1974 (Fig. 3.3; Table 3.3). In the 12-month comparison that distinguished between ripe and unripe materials, only ripe seed was significantly different between 2000-01 and 1988-89: the mangabeys ate more ripe seed in 2000-01 (Fig. 3.4; Table 3.3). The groups in 2000-01 and 1988-89 also differed from the group in 1974 in the percentage of animal matter in the diet, which increased from the earliest to the later studies (Fig. 3.3; Table 3.3).

Although there was no difference in percent contribution to the diet of stem/new growth among the three studies (Fig. 3.3; Table 3.3), there was a significant increase between 1988-89 and 2000-01 when twelve months of data were compared (Fig. 3.4;

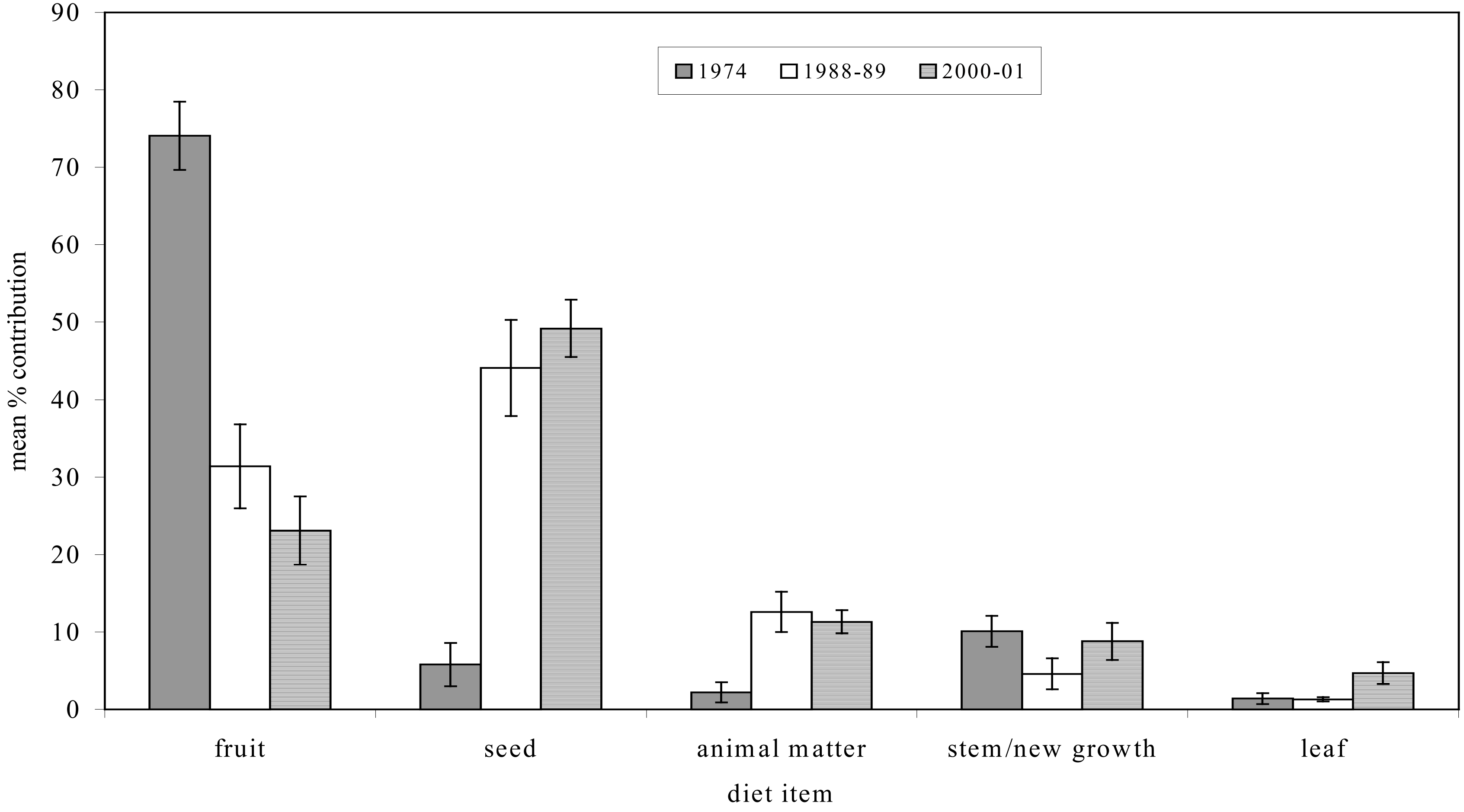

Fig. 3.3. Mean percent contribution to the seven-month diet of the main diet items in 1974, 1988-89, and 2000-01. Error bars display plus or minus one standard error from the mean.

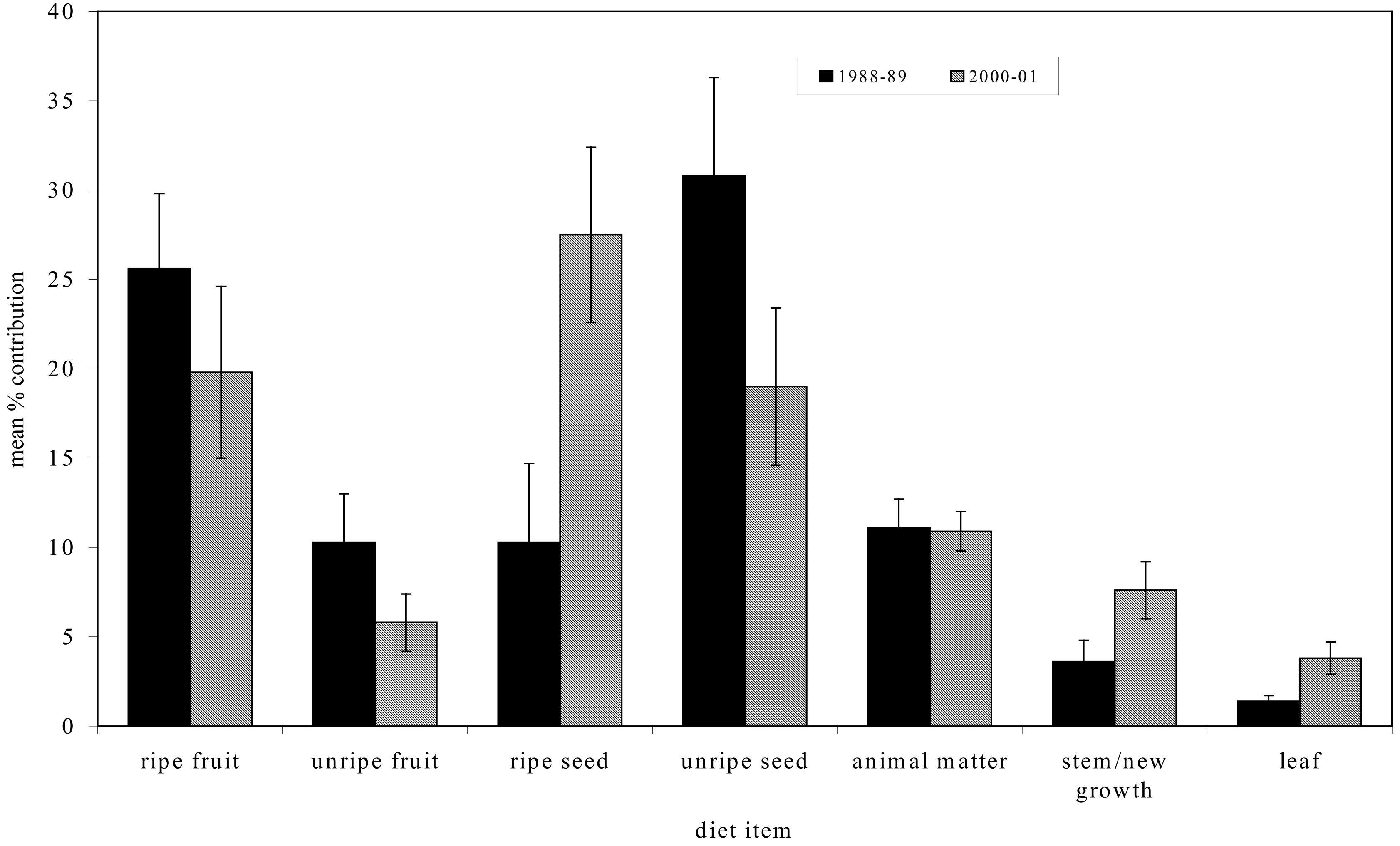

Fig. 3.4. Mean percent contribution to the annual diet of the main diet items in 1988-89 and 2000-01. Error bars display plus or minus one standard error from the mean.

Table 3.3. Results of statistical tests comparing five diet items among three studies, and seven diet items between two studies. Significant differences were found with post hoc Wilcoxon Signed Ranks tests ($p < 0.05$).

	1974 vs. 1988-89 vs. 2000-01			1988-89 vs. 2000-01		
Diet item	F or χ^2	p	Significant differences	Z or t	p	Significant difference
Fruit[a]	33.077	0.0005	2000 & 1988 > 1974			
Ripe fruit[b]				-0.706	0.480	no difference
Unripe fruit[c]				1.382	0.194	no difference
Seed[a]	28.406	0.0005	2000 & 1988 > 1974			
Ripe seed[b]				-2.237	0.025	1988 < 2000
Unripe seed[c]				1.772	0.104	no difference
Animal matter[c,d]	7.714	0.021	2000 & 1988 > 1974	0.108	0.916	no difference
Stem/new growth[a,b]	1.777	0.198	No differences	-2.490	0.013	1988 < 2000
Leaf[a,b]	4.384	0.028	2000 > 1974 & 1988	-2.228	0.026	1988 < 2000

[a] analyzed by One-Way ANOVA (F); df = 2,18

[b] analyzed by Wilcoxon Signed-Ranks Test (Z)

[c] analyzed by t Test (t); df = 11

[d] analyzed by Friedman Test (χ^2); df = 2

Table 3.3). The group in 2000-01 also ate more leaves than either the group in 1988-89 or in 1974 (Fig. 3.3; Table 3.3).

Ecological Comparisons

Of the 25 plant species counted throughout the group's range in both 1988-89 and 2000-01, six species were never observed to be eaten by the Mchelelo West group or never appeared in the top five in any month for any of the three studies. For the remaining 19 food species, there was no significant change in density of these plants in the respective ranges of the Mchelelo West mangabey group in 1988-89 and in 2000-01. Thirteen species in common with those compared between 1988-89 and 2000-01 were measured in 1975 and 1988. There also was no significant change in density of these 13 species between 1975 and 1988.

There was no significant change in fruit availability (using a composite of mean monthly fruit score and species density) in six species compared between 1974 and 1988-89. There was also no significant difference in biomass (mean monthly fruit score x species density x species mean DBH) of total fruit, unripe fruit, or ripe fruit in seven species compared between 1988-89 and 2000-01.

Correlations Between Diet Item Availability and Consumption

There was no significant positive relationship between ripe fruit availability and consumption in seven species in 2000-01. There was a negative correlation between ripe fruit availability and consumption of unripe fruit (r = -0.554; *p* = 0.031). There were no significant negative correlations between abundance of ripe fruit and consumption of the other two diet items (i.e., ripe seeds or unripe seeds).

When the seven species were analyzed together, there were no significant positive correlations between availability and consumption of any of the diet items. When the species were examined individually, however, significant correlations were determined (Table 3.4). There was a significant correlation between ripe fruit consumption and ripe fruit availability in four of the seven species analyzed individually: *P. reclinata*, *D. mespiliformes*, *S. madagascariensis*, and *F. sycomorus*. Consumption of ripe seed was significantly correlated with availability for *P. reclinata* and *A. robusta*. In addition, there were significant correlations between unripe fruit consumption and availability in *S. madagascariensis* and *F. sycomorus* and between unripe seed consumption and availability in *P. reclinata* and *S. madagascariensis*. *H. compressa* and *O. spinosa* did not show any significant correlations between consumption and availability of any of the diet items.

DISCUSSION

When behavioral and dietary changes were investigated among three studies of a group of Tana mangabeys over a period of 27 years, the group in 2000-01 was more similar to the group in 1988-89 than it was to the group in 1974. In addition, all comparisons using a sub-sample of seven months of data between the groups in 1988-89 and 1974 agree with comparisons made by Kinnaird (1990) using all 15 months of her data.

Table 3.4. Spearman's rank correlation coefficients for consumption (percent monthly frequency) and availability (mean monthly phenology score) of four diet items per species in the diet of the group in 2000-01.

Species	Ripe fruit	Ripe seed	Unripe fruit	Unripe seed
Phoenix reclinata	0.684**	0.522*	0.324	0.777**
Acacia robusta	n.e.	0.502*	n.e.	0.346
Hyphaenae compressa	0.125	0.093	n.e.	0.401
Oncoba spinosa	-0.042	n.e.	0.117	n.e.
Diospyros mespiliformes	0.506*	0.349	0.151	0.239
Sorindea madagascariensis	0.631*	0.243	0.731**	0.721**
Ficus sycomorus	0.733**	n.e.	0.695**	n.e.

* $p < 0.05$, ** $p < 0.01$, one-tailed
n.e. = not eaten

In examining the temporal similarities and differences, I will first discuss the comparison of diet items, as dietary strategies impact other aspects of behavior (Oates, 1987). The mangabey group in 1988-89 ate fewer fruits, especially ripe, and more seeds, especially unripe, than the group in 1974 (Kinnaird, 1990). Kinnaird (1990) hypothesized that ripe fruits had become less available by 1988-89, and as a consequence the group in 1988-89 switched from ripe fruit to unripe seeds to compensate for lower food availability. Support for such a hypothesis could be seen in other research where preference for fruit, and the subsequent switching to different diet items when fruit is not available, has been observed in a number of primate taxa on a seasonal basis: *Cebus apella*, *C. albifrons*, *Saimiri sciureus*, *Saguinus imperator*, and *Saguinus fuscicollis* (Terborgh, 1983); *Cercopithecus sabaeus* (Harrison, 1984); *Macaca fascicularis* (Lucas and Corlett, 1991); *Saguinus fuscicollis avilapiresi*, *S. mystax pileatus*, *Cebus apella*, and *Lagothrix lagotricha cana* (Peres, 1994); *Cebus apella* (Zhang, 1995); *Pan paniscus*

(Wrangham *et al.*, 1998); *Lophocebus albigena* (Poulsen *et al.*, 2001); and *Cercopithecus nictitans*, *C. pogonias*, and *Lophocebus albigena* (Brugiere *et al.*, 2002).

Given that the group in 2000-01 continued to consume less fruit and more seeds relative to the group in 1974, consistent with Kinnaird's findings for the group in 1988-89, additional data are available to begin assessment of the hypothesis of a decline in ripe fruit availability resulting in a compensatory switch to unripe seeds. Evidence supporting this hypothesized explanation is lacking. There were no significant changes in fruit abundance among the three studies; fruit was not more abundant in 1974 when the group's diet consisted predominantly of fruit compared to later years when the diet was significantly composed of seeds.

A requisite corollary of the hypothesis is that the Tana mangabey prefers ripe fruit, consuming more or less of this particular diet item in relation to changes in its availability. If this preference could be supported, and if Kinnaird's hypothesis holds, then the groups should consume ripe fruit in correlation to its availability <u>and</u> increase their consumption of other diet items (i.e., ripe or unripe seeds, unripe fruit) only as ripe fruit abundance decreases. Limitations to the data presented by Homewood (1976) and Kinnaird (1990) preclude testing this prediction between their two studies, but the proposed changes in consumption and availability could be examined with data for the group in 2000-01. Contrary to the prediction, there is no evidence of a positive correlation between availability and consumption of ripe fruit <u>in conjunction with</u> negative correlations between ripe fruit availability and consumption of other diet items. The mangabeys are not concentrating their diet on ripe fruit, contrary to what early studies may have suggested. They are not eating more fruit when it is more readily available, and they do not appear to consume all other diet items only in compensation for declines in fruit availability.

An alternative hypothesis might be that the mangabeys consume the various items in their diet (ripe fruit and seeds, unripe fruit and seeds) in relation to each item's availability. This was supported for certain diet items and for some individual plant species in the dietary analysis for the group in 2000-01. The evidence for dietary breadth and flexibility in this mangabey (Homewood, 1976; Kinnaird, 1990; this study), in combination with such consumption of diet items on a species-specific availability basis, would compensate for seasonality of overall fruit production and the varying fruiting schedules of individual species, insuring adequate resource consumption on an annual and more long-term basis. Such ecological flexibility should also contribute to the Tana mangabey's viability in the characteristically fragmented, dynamic, and diverse habitat that they occupy.

Nutritional analyses of the diet items eaten by the mangabeys could also advance the investigation of dietary choice and changes in this species. Although Kinnaird (1990) considered the diet of the group in 1988-89 to be of lower quality than that of the group in 1974 because of the former group's high consumption of seeds, it may be premature to conclude that seeds are of lower quality before undertaking such nutritional analyses. In some studies, seeds have been found to be higher in fats, proteins, and minerals than fruit (Janson and Chapman, 1999); to offer more energy per hectare per year than fruit (Janson and Emmons, 1990); and to be higher in protein and lower in fiber (Dasilva, 1992; Barton *et al.*, 1993), as well as higher in calories (Dasilva, 1992), than fruit. The additional fact that there are observations of the group in 2000-01 discarding or ignoring ripe fruit pulp to eat ripe seeds (pers. obs.) further suggests that nutritional analyses of mangabey food items would be valuable. *A. robusta*, the second-ranking diet species in 2000-01 (unpub. data) and a legume in the family Mimosaceae, should also be investigated for its contribution to the significance of seeds in the mangabey diet. Seeds from legumes have been found to be important in the diets of other primates (e.g., *Colobus a. angolensis* and *C. badius tholloni* in Central Zaire: Maisels *et al.*, 1994; *C. polykomos* in Sierra Leone: Dasilva, 1992). In addition, the density of this species increased six-fold in the group's range between 1988-89 and 2000-01 (unpub. data). As leguminous species are known to grow well under conditions of lower soil quality (e.g., Maisels *et al.*, 1994), the ecological factors associated with this increase in density should also be examined.

In the examination of behavioral differences, the group in 1974 differed from the groups in 1988-89 and 2000-01 in the mean time spent in four behaviors, devoting less time to eating and foraging and more time to moving and being inactive. The group in 1988-89 differed from the group in 2000-01 only in spending more time in social/sexual behavior and less time in inactive behavior, and only when 12 months of data were analyzed. There are several possible reasons why these groups differed in their activity budgets. According to foraging theory, when food abundance is constant larger groups should eat, forage, and move more and rest less than smaller groups due to increased costs of social foraging (van Schaik *et al.*, 1983; Stacey, 1986; Watts, 1988; Chapman, 1990; Lawes and Piper, 1992; Isbell and Young, 1993), although exceptions do occur (e.g., de Ruiter, 1986; O'Brien and Kinnaird, 1997). The largest mangabey group (50 individuals, this study) did in fact eat and forage more and rest less than the next largest group (36 individuals, Homewood, 1976), although they spent less time moving. The smallest of the three groups (17 individuals, Kinnaird, 1990), however, was more similar in behavior to the largest group than the group intermediate in size, differing from the largest group only in being less inactive, opposite that expected from foraging theory. Although a lower fruit availability for the group in 1988-89 could result in the observed difference in activity, from the analyses presented here, there is no evidence that the group in 1988-89 suffered from lower fruit availability than the group in either 1974 or in 2000-01.

Primate groups may also differ in activity budgets because of different diets; particular diet items put distinct demands on behavior. For example, groups that subsist on foliage will forage and move less, and rest more, than groups subsisting on fruit, flowers, and animal matter, due to foliage being more abundant, evenly distributed, and difficult to digest (Clutton-Brock and Harvey, 1977; Struhsaker, 1980; Terborgh, 1983). Lower quality diet items, less dense food resources, and a less productive habitat may also cause a group to feed, forage, and move more in order to acquire enough nutrition (Iwamoto and Dunbar, 1983; Watts, 1988; O'Brien and Kinnaird, 1997). The mangabey groups in 1988-89 and 2000-01 did differ in their diet from the group in 1974, eating less fruit and more seeds and animal matter. As many of the unripe and ripe seeds they eat require manipulation, an increase of seeds in the diet will increase foraging time, which was observed in the groups in 1988-89 and 2000-01. An increase in animal matter could also have increased foraging time. These two groups also increased time spent eating over the group in 1974. Kinnaird (1990) hypothesized this was due to the lower-quality diet of seeds versus fruit, but this cannot be assumed until nutritional analyses are undertaken, as discussed above. A lower quality diet (with no change in distribution of food) would also predict increased time spent moving, and this was not the case for the group in 2000-01 or 1988-89. Alternatively, the increase in leaf and stem/new growth seen in the diet of the group in 2000-01 may help explain the increase in time inactive seen between that study and the other two as those items require longer periods of digestion (Oates, 1987).

Although ecological explanations are limited for the dietary shifts we have observed in the Tana mangabey, the three studies that have investigated mangabey diet have all concluded that they are flexible in their dietary choices. As a response to habitat loss and degradation occurring in the lower Tana River forests, this flexibility may decrease the mangabeys' vulnerability. Wieczkowski and Mbora (2002) reported a mean mangabey group size of 30.4 (n = 17 across 10 forests in the Tana), an increase from 20.5 in 1988-89 (n = 7; Kinnaird and O'Brien, 1991) and 26.5 in 1973-74 (n = 4; Homewood, 1976). This is despite drastic loss and degradation of forest in the period 1994-2000, and in contrast to the significant decrease in mean group size in the Tana River red colobus from pre-1994 counts (Wieczkowski and Mbora, 1999-2000). The mangabey's ecological flexibility, especially in their diet, can be posited as a reason why they have not responded to the forest loss with a population decline – at least not to this point in time. Decker and Kinnaird (1992) cited the same reason to explain why the mangabeys had suffered a less severe population loss than the red colobus between 1974-75 and 1987. Behavioral research on mangabey groups living in forests that are suffering from anthropogenic habitat change would be helpful in further investigating the mangabeys' ecological flexibility, especially to determine how they are able to respond to habitat change "in progress." This should be accomplished by additional study of the forests on the east bank of the Reserve and at the southern limit of the mangabeys' distribution, where human activity and disturbance are greater than in the forests comprising the range of the groups studied to date.

The Tana mangabey, however, is clearly a forest primate; the mean number of mangabey groups per forest is significantly associated with forest area and density of trees ≥ 10 cm DBH (Wieczkowski, in prep. a). Regardless of the present mangabey population, and the degree of ecological flexibility documented for this highly endangered species, protection of forest area should be the primary concern of management for the health of the biodiversity of the lower Tana River.

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CHAPTER 4

AN EXAMINATION OF THE INCREASED ANNUAL RANGE OF A TANA MANGABEY (*Cercocebus galeritus*) GROUP[1]

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[1] Wieczkowski, J. To be submitted to *American Journal of Physical Anthopology*.

ABSTRACT

A group of Tana mangabeys (*Cercocebus galeritus*) has greatly expanded its annual range over three decades: from 17.25 hectares in 1974 (Homewood, 1976) and 18.75 hectares in 1988-89 (Kinnaird, 1990) to 46.75 hectares in 2000-01. Utilizing 5-minute mapping samples (n = 817), phenological samples (n = 960), vegetation data, and statistical and descriptive comparisons with previous data, I tested six non-mutually exclusive hypotheses concerning this range increase. The hypotheses of the departure of neighboring mangabey groups, a decrease in population density, a decrease in density of food trees, and an increase in coverage in non-forest corridors are not supported. There is support for the hypothesis of a decrease in fruit availability per hectare. Four of six individual species, plus all eight species combined, compared between Kinnaird's (1990) and this study showed significant decreases. The hypothesis with the strongest support is an increase in group size. Group size decreased from 36 in 1974 to 17 in 1988-89, but is now 50 individuals. This hypothesis is also supported by an equivalent food tree abundance per capita in the increased range and a significant increase in average daily distance since Kinnaird's (1990) study. Other evidence, however, supports the idea that home range increased prior to the increase in group size.

Abbreviated title: Increased range of a Tana mangabey group

Key words: home range; group size; temporal change; critically endangered primate; management

INTRODUCTION

The use of space by primates is determined by several factors, among them resource abundance and distribution (e.g., Clutton-Brock, 1975; Di Bitetti, 2001), group size and social organization (e.g., Takasaki, 1984; Isbell, 1991), presence of conspecific groups (e.g., Kinnaird, 1990; Barrett and Lowen, 1998), and the location of important resources such as sleeping sites and waterholes (e.g., Altmann and Altmann, 1970; Barton et al., 1992). In studying use of space by primates, a number of social, cognitive, and ecological factors must be considered (Boinski and Garber, 2000), and investigation can focus on one group through seasonal changes (e.g., Di Bitetti, 2001), conspecific groups in different habitats (e.g., Freeland, 1974), similar but more distantly related species (e.g., Kinnaird and O'Brien, 2000), or a single group studied longitudinally (e.g., Olupot et al., 1994).

The Mchelelo West group of Tana mangabeys (*Cercocebus galeritus*) has been the subject of three studies over a 27-year period. The most readily observed change exhibited by this group is the expanded size of its home range. Whereas in 1974 (Homewood, 1976) and in 1988-89 (Kinnaird, 1990) the group was limited to ranging within only one of the forests within the fragmented and dynamic Tana River landscape, Mchelelo West forest, the group in 2000-01 ranged over three forested habitats: Mchelelo West forest as well as Mchelelo Research Camp and Guru South forest. Six non-mutually exclusive hypotheses can be posited with regard to the ecological or demographic changes that might be associated with this increase in home range size:

H1: There was a departure of neighboring mangabey groups.

Both Homewood (1976) and Kinnaird (1990) found that the presence of another mangabey group in Mchelelo West forest restricted the range of the Mchelelo West study group. During both studies, another group entered Mchelelo West forest from the south and almost entirely overlapped the study group's range. Homewood (1976) found both day range and monthly range of the Mchelelo West group to be negatively correlated with the number of calls given by the other group on a daily or monthly basis. Kinnaird (1990) found that when the other group was in Mchelelo West forest, the Mchelelo West group backtracked more and had smaller monthly ranges than when the other group was absent. It is possible that this mangabey group to the south acted as a 'social barrier' (Barrett and Lowen, 1998); the presence of the neighboring group may have prevented the study group from expanding into that area, resulting in a smaller home range as long as that neighboring group was present. The increased home range of the Mchelelo West mangabey group in 2000-01 might therefore be associated with the departure of neighboring mangabey groups, and therefore the relaxation of 'social barriers'.

H2: There was an increase in group size.

Feeding competition, an automatic and universal cost of group living (Alexander, 1974), is potentially more intense in larger groups than in smaller groups, reducing the per capita foraging efficiency of group members (Terborgh and Janson, 1986). In order to obtain adequate food resources, a larger group will therefore need to use more space than a smaller group if food abundance is constant (Terborgh, 1983). Interspecific comparisons have found a positive relationship between group size and home range size (Milton and May, 1976; Isbell, 1991), as well as between population group weight and home range size (Clutton-Brock and Harvey, 1977b). Positive relationships between group size and home range size have also been found in intraspecific comparisons: *Alouatta pigra* (Ostro et al., 1999), *Macaca fuscata* (Takasaki, 1981, 1984), *Papio* *cynocephalus* (Stacey, 1986), and *Theropithecus gelada* (Iwamoto and Dunbar, 1983). The increased home range of the Mchelelo West mangabey group in 2000-01 could be associated with such an increase in group size. A corollary to this hypothesis is that an increase in group size also would be associated with an increase in daily distance traveled (Clutton-Brock and Harvey, 1977b; Waser, 1977; Sharman and Dunbar, 1982; Iwamoto and Dunbar, 1983; van Schaik et al., 1983; de Ruiter, 1986; Olupot et al., 1994; Ostro et al., 1999). By increasing home range and daily travel distance, individual members of large groups can gain access to an equivalent amount of resources as individuals of smaller groups.

H3: There was a decrease in population density.

Intraspecific comparisons for a number of primate taxa have found that population density and home range size are negatively correlated: *Alouatta pigra* (Ostro et al., 1999), *Cercopithecus mitis* (Butynski, 1990), *Colobus guereza* (Dunbar and Dunbar, 1974), *C. satanas* (Fleury and Gautier-Hion, 1999), *Macaca sylvanus* (Mehlman, 1989), and *Procolobus badius rufomitratus* (Decker, 1994). A larger home range is generally interpreted as a consequence of fewer intergroup encounters associated with lower population density (Butynski, 1990; Ostro et al., 1999), although population density can be confounded with habitat quality (Clutton-Brock and Harvey, 1977a; Mehlman, 1989; Butynski, 1990). The increased home range of the Mchelelo West mangabey group in 2000-01 could therefore be associated with a decrease in population density.

H4: There was a decrease in food availability in the previous range, resulting from changes in abundance.

H4a: There was a decrease in density of food trees in the previous range.

Both interspecific (Clutton-Brock and Harvey, 1977a) and intraspecific (*Cercopithecus aethiops*: Gartlan and Brain, 1968; Lee and Hauser, 1998; *Colobus guereza*: Takasaki, 1981; *Colobus satanas*: Fleury and Gautier-Hion, 1999; *Macaca fuscata*: Takasaki, 1984; *Macaca mulatta*: Neville, 1968; Takasaki, 1984; *Macaca nemestrina*: Caldecott, 1986; *Macaca sylvanus*: Mehlman, 1989) comparisons have found that home range size is inversely correlated with habitat quality. As density of food trees decreases, a group must cover a wider area in order to obtain adequate food. The increased home range of the Mchelelo West mangabey group in 2000-01 could therefore be predicted to result from a decrease in density of food trees in the previous range.

H4b: There was a decrease in fruit availability per hectare in the previous range.

Another manner in which a habitat may be of lower quality is if fruit availability per hectare decreases, necessitating a larger home range. The increased home range of the Mchelelo West mangabey group in 2000-01 could therefore be associated with a decrease in fruit availability per hectare in the previous range.

H5: There was an increase in basal area coverage (m^2/tree or m^2/ha/tree) in non-forest corridors.

Based on their observations, Homewood (1976) and Kinnaird (1990) concluded that the Mchelelo West mangabey groups in 1974 and 1988-89, respectively, were limited in their home ranges by the size of Mchelelo West forest; the group did not move far outside the boundaries of the delineated area of forest. Although the forest is larger now (26 hectares as opposed to 17), the increased range of the group in 2000-01 encompassed two additional forested areas beyond the boundaries of the larger Mchelelo West forest. The group in 2000-01 moved through two areas of non-forest, an area between Mchelelo West forest and Mchelelo Research Camp and an area to the south of Mchelelo West forest. During the previous studies, the study group did not travel through these areas (Homewood, 1976; Kinnaird, 1990; Medley, 1990). Other mangabey species have been observed to move through savanna to visit forest fragments (*C. albigena*: Tutin et al., 1997; Tutin, 1999) and to use abandoned farm clearings (*C. atys*: Fimbel, 1994). The increased home range of the Mchelelo West mangabey group in 2000-01 could therefore be associated with an increase in overall tree basal area coverage in corridors connecting Mchelelo West forest to other areas to the north and south, permitting or facilitating group movement between previously more isolated fragments.

The research reported here takes a longitudinal approach in examining each of these hypotheses, utilizing data from the two earlier studies (1974 and 1988-89) and newly collected data (2000-01) for this group.

METHODS

Study Area and Group

The study was part of a broader examination of the habitat requirements and ecological flexibility of the Tana mangabey, and was conducted within the Tana River Primate National Reserve in southeastern Kenya (1°45’ to 2°00’ S, 40°07’ E) (Fig. 4.1).

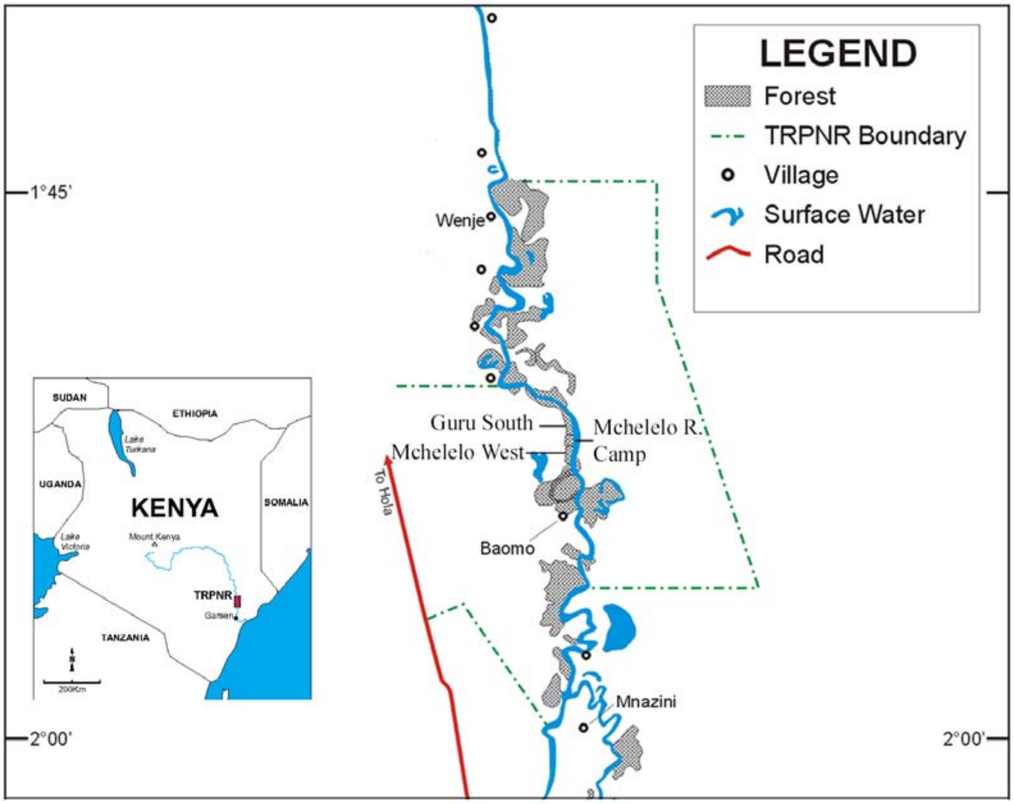

Fig. 4.1. The Tana River Primate National Reserve (TRPNR), with study forests named. Adapted from Mbora (2003).

Data collected on one of the mangabey groups previously studied by Homewood (1976) and Kinnaird (1990) permitted investigations of changes in behavior and diet, and attempts to link these to concomitant changes in the habitat of the group (particularly food abundance) (see Wieczkowski, in prep. b).

The forests within the Reserve are riverine forest, dependent on inundation, sediment transport, erosion, and alluvial deposition of the Tana River, as well as groundwater level (Medley, 1990). The lower Tana River receives a mean annual precipitation of only 582 mm (averaged by month for 38 months 1996-2001; unpublished climatological data, Mchelelo Research Camp), and is therefore classified as an arid/semi-arid area. The short rains occur in November and December, while the long rains occur from March through June. The mean daily minimum temperature is 23.1°C and the mean daily maximum temperature is 32.9°C; the coldest months are June and July, while the warmest months are January-March (unpublished climatological data, Mchelelo Research Camp).

The 169 km^2 Reserve was gazetted in 1976 to protect populations of the Tana mangabey and Tana River red colobus (*Procolobus rufomitratus*), and their riverine forest habitat. The Reserve is positioned in the northern 30 kilometers of the primates' 60-kilometer distribution. Both of these species were recently included in the list of the 25 most endangered primates (Mittermeier and Konstant, 2002), are classified as "Critically Endangered" (IUCN, 2000), and are listed as CITES Appendix I Taxa (IUCN, 1996).

In 2000-01, the study group ranged in the 19.25 hectare Guru South forest, the 8 hectare Mchelelo Research Camp, and the 26 hectare Mchelelo West forest (Fig. 4.1).

Although this is the same group studied in 1988-89 by Kinnaird (1990) and in 1974 by Homewood (1976), during these previous studies the group did not range outside Mchelelo West forest. I will refer to the group as the Mchelelo West group.

Ranging

Data were collected on the mangabey group from 0700 to 1815 hours in one block of three days per month, for a total of 12 3-day samples during the time period August 2000 to July 2001. Kinnaird (1990) collected data in one block of three days per month for 15 months, from January 1988 until March 1989. Homewood (1976) collected data in one block of five days per month for seven months, from February until August 1974. As new entries into quadrats had reached an asymptote in both Homewood's (1976) and the current study, the difference in number of observation days should not have any significant effect on determination of the group's ranging behavior.

Every half-hour, I spent five minutes marking the location of each individual on scaled maps drawn for each of the forests (Homewood, 1976; Kinnaird, 1990) (n = 817 five-minute samples). For each five-minute sample, I determined the group's center of mass as the center of a polygon including all sighted animals (Waser and Floody, 1974; Homewood, 1976; Kinnaird, 1990). Half-hour distance was measured as the distance moved between consecutive centers of mass. There were a few instances when I lost the group for one mapping sample; in those cases, I divided the hour distance by two to obtain the half-hour distance. Half-hour distances were summed each day to arrive at a daily distance traveled (Homewood, 1976; Kinnaird, 1990). For each three-day sample, I calculated a mean daily distance (mean of the daily values for each of the three days).

For the one sample in which I lost the group for half of a day, I did not include that daily distance in the mean.

Statistical analysis of daily distance is limited to comparison between quantitative ranging data from the current study and Kinnaird's (1990), after a February 1988-January 1989 sub-sample was taken from the latter. Homewood (1976) did not present quantitative ranging data that permitted comparative statistical analysis; i.e., mean daily distance traveled in each sample. A Paired-Samples *t* Test (one-tailed) was used to determine if there was an increase in the mean daily distance traveled. A 50 m by 50 m (0.25 hectare) grid was superimposed over the range maps, and the grids in which at least one mangabey was sighted were noted. The number of unique 0.25 hectare quadrats entered during all observations was counted to arrive at an annual range (Homewood, 1976; Kinnaird, 1990).

Neighboring Groups, Group Size, and Population Density

During the current study, neighboring groups to the Mchelelo West group were not observed systematically and their home ranges were not measured. Location of these groups was noted through vocalizations and sightings collected on an ad-lib basis during the 3-day samples on the Mchelelo West group. Departure of these groups from the previous range was determined based on these ad-lib samples.

An attempt was made during each 3-day sample to obtain a complete group count of the study group. A mean was calculated of complete counts ($n = 23$) throughout the study period; counts were considered complete based on their quality (group passing over a trail or through a break in the canopy) and general agreement with previous and subsequent counts. Mean group counts are also available from Homewood (1976) and Kinnaird (1990).

Population densities (number of individuals per hectare) in all three studies were calculated by multiplying the size of each group using an area by the proportion of days that group spent in an area divided by the area's size. Presence of each of two other groups that shared the study group's home range in 2000-01 was noted by sight or vocalizations during the 3-day follows. The proportion of days each group was present during 2000-01 was calculated as the number of days they were observed divided by the number of observation days. Repeated group size counts of the neighboring groups were collected as often as possible throughout the study period. Kinnaird (1990) presented group sizes for the two groups that used Mchelelo West forest, and the proportion of days the southern group was in Mchelelo West forest. Homewood (1976) presented only group sizes for the two groups that used Mchelelo West forest; the proportion of days the southern group was in the forest during Homewood's (1976) study was estimated based on the mean proportion of days that group spent in the forest in 1988-89 (44.9%; Kinnaird 1990) and 2000-01 (43.9%; this study).

Food Tree Density

Mchelelo West forest has a system of clearly marked quadrats of 0.25 hectare. Within 65 quadrats (16.25 hectares), I enumerated all reproductively-sized individuals of 23 liana, palm, sub-canopy tree, and canopy tree species. Kinnaird (1990) had collected data on the same 23 species from the same 65 quadrats, which comprised the entire forested range of the group in 1988-89; Homewood (1976) did not collect comparable data. The 23 species were selected because they appeared in the Mchelelo West group's diet in at least one of the studies (Homewood, 1976; Kinnaird, 1990; Wieczkowski, in prep. b). Density was calculated by dividing the total number of individuals counted of each species by the total number of hectares sampled. A one-tailed Wilcoxon Signed Ranks Test was used to determine if there was a significant decrease in total species density in Mchelelo West forest between the two time periods for which data are available.

Although a decrease in food tree density in the former range could be predictive of an increase in home range, a better measure would incorporate any changes in size of the group utilizing the area and therefore the abundance of food trees "available" to each individual. As such, the count of food trees was also converted to abundance per individual of the study group and compared between time periods, again utilizing the one-tailed Wilcoxon Test.

Fruit Availability

Ten individual trees from each of nine species were monitored for phenological activity in Mchelelo West forest on the day immediately prior to or subsequent to each 3-day sample of the group. The individual trees were randomly selected from within four belt transects randomly placed within the forest as part of an investigation of forest attributes and mangabey abundance (Wieczkowski, in prep. a). These nine species were selected through the following process. A list of the top fifteen diet species was created by averaging the percent contributions of each diet species (fungi and grass excluded) across the five mangabey groups previously studied (Homewood, 1976; Kinnaird, 1990).

These averages were then ranked and the top fifteen species noted. Homewood (1976) found that percent contribution to the diet was significantly correlated to canopy abundance for the top twenty food species eaten by the mangabey groups she studied. I therefore determined the abundance (see Wieczkowski, in prep. a, for methods of determining abundance) of each of the top fifteen diet species in Mchelelo West forest, and selected the nine most abundant. The nine most important food species in the diets of the mangabey groups studied previously comprised a significant proportion of their annual diet (range 69%-92.8%; Homewood, 1976; Kinnaird, 1990), and was therefore considered to be an adequate sample to test for the relationship between food abundance and ranging. The presence of fruit was scored on a 0-5 scale measuring the estimated percentage of total possible coverage (0 = 0%, 1 = 1-20%, 2 = 21-40%, 3 = 41-60%, 4 = 61-80%, 5 = 81-100%) (Homewood, 1976). These scores were summed by species within each month and divided by the number of trees sampled to arrive at a mean monthly fruit score for each species. Because density of trees can influence fruit abundance habitat-wide (Harrison, 1984; Chapman et al., 1994) and DBH has been found to be an accurate estimate of fruit number and/or biomass (McDiarmid et al., 1977; Leighton and Leighton, 1982) or crown volume (Phillips, 1995) the mean monthly fruit scores were multiplied by the species density and the mean DBH of all trees monitored of the species to estimate biomass of available fruit per hectare (mean monthly fruit score x density x mean DBH).

Because Homewood (1976) had collected neither DBH nor density data, comparisons of fruit availability per hectare were not undertaken with that study. Kinnaird collected phenology data on eight species (*Acacia robusta*, *Diospyros* *mespiliformes*, *Ficus sycomorus*, *Hyphaenae compressa*, *Phoenix reclinata*, *Oncoba spinosa*, *Alangium salviifolium*, and *Sorindea madagascariensis*) in common with the current study, and also measured the DBH of each tree in her phenology sample. In order to compare to the year's worth of data collected in the current study, biomass estimates were calculated from Kinnaird's data (unpublished; provided with permission) utilizing only her February 1988-January 1989 phenological samples. Values for the first six species were compared between the two studies with a Paired-Samples *t* Test; *A. salviifolium* and *S. madagascariensis* could not be tested statistically because of a prevalence of zeros. A comparison of all eight species combined was undertaken with a Wilcoxon Signed Ranks Test. The hypotheses of decreases in mean fruit scores were tested with one-tailed tests.

Basal Area Coverage in Non-Forest Corridors

I collected vegetation data from two non-forest areas that the mangabey group in 2000-01 moved through to determine if these areas had more basal area coverage than non-forest areas through which the group in 1988-89 did not move. A belt transect of 160 meters long by 5 meters wide (0.08 hectares) was sampled in the Mchelelo West-Mchelelo Research Camp corridor (MCHW-MRC), and a belt transect of 410 meters long and 5 meters wide (0.205 hectares) was sampled to the south of Mchelelo West forest (MCHWTrail10). Both of these transects followed exact pathways the mangabey group traveled during observations. For each tree or palm three meters or taller within each transect, I measured the DBH of each stem. Each DBH measurement was converted to basal area (m^2/tree) by using the equation for area of a circle (πr^2) and converting from

cm^2 to m^2. If the tree or palm had more than one stem, the basal area of each individual stem was calculated and then summed for basal area of the tree. Basal area per tree (m^2/tree) measures the size of individual trees regardless of how many trees there are; a larger mean basal area per tree indicates larger trees. For the measure m^2/ha/tree, each m^2/tree value was divided by the number of hectares sampled in the belt transect. Basal area per hectare per tree (m^2/ha/tree) attempt to assess the thickness of the vegetation in the corridor; a larger mean basal area per hectare per tree indicates more of the hectare has coverage, whether by larger trees or more bushes.

I compared the data I collected in non-forest areas the group in 2000-01 moved through to data collected by Medley (1990) in non-forest areas, to the north of Mchelelo West forest (Mchelelo North) and to the south of the forest (Mchelelo South). Neither of these areas was used by the Mchelelo West mangabey group in 1988-89 (although the southern area was used by another mangabey group) (Kinnaird, 1990; Medley, 1990).

A two-tailed Kruskal-Wallis Test was performed to determine if there were differences among these four non-forest areas in mean basal area per tree (m^2/tree) or in mean basal area per hectare per tree (m^2/ha/tree). As mangabeys are able to pass through non-forested corridors of both types (large trees with no undergrowth and thick, shrubby areas; pers. obs.), increases in either of these measures may have allowed the mangabey group to use these corridors. One-tailed Mann-Whitney Tests were performed on each of the four pairs (MCHW-MRC and Mchelelo North; MCHW-MRC and Mchelelo South; MCHWTrail10 and Mchelelo North; and MCHWTrail10 and Mchelelo South) to determine if the MCHW-MRC area or the MCHWTrail10 area used by the group in 2000-01 had a larger mean basal area per tree or a larger mean basal area per hectare per tree values than the Mchelelo North or Mchelelo South areas not used by the group in 1988-89.

RESULTS

Ranging

The mangabey group in 2000-01 entered 187 0.25 hectare quadrats during the observation months, an annual range of 46.75 hectares (Fig. 4.2). This included Guru South forest, Mchelelo Research Camp, and Mchelelo West forest. The group in 1988-89 had a range of 18.75 hectares (Kinnaird, 1990; Fig. 4.3) and the group in 1974 had a range of 17.25 hectares (Homewood, 1974; Fig. 4.4). During both of the earlier studies, the group ranged entirely within the Mchelelo West forest.

The group in 2000-01 had a mean daily distance of 1395 ± 49 meters, significantly longer than in 1988-89 (1184 ± 39 meters) ($t = 5.472$; df = 11; $P < 0.0005$). The 1974 median daily distance was 1040 meters over 7 months (Homewood, 1976), less than either of the other two time periods.

H1: There was a departure of neighboring mangabey groups.

The neighboring mangabey group to the south of the Mchelelo West group's range was still present in 2000-01, and ranged as far north as it did in 1988-89 (Kinnaird, 1990). In addition, the neighboring group to the north ranged within Mchelelo West forest in 2000-01, as well as overlapping with the study group in Mchelelo Research Camp and Guru South forest.

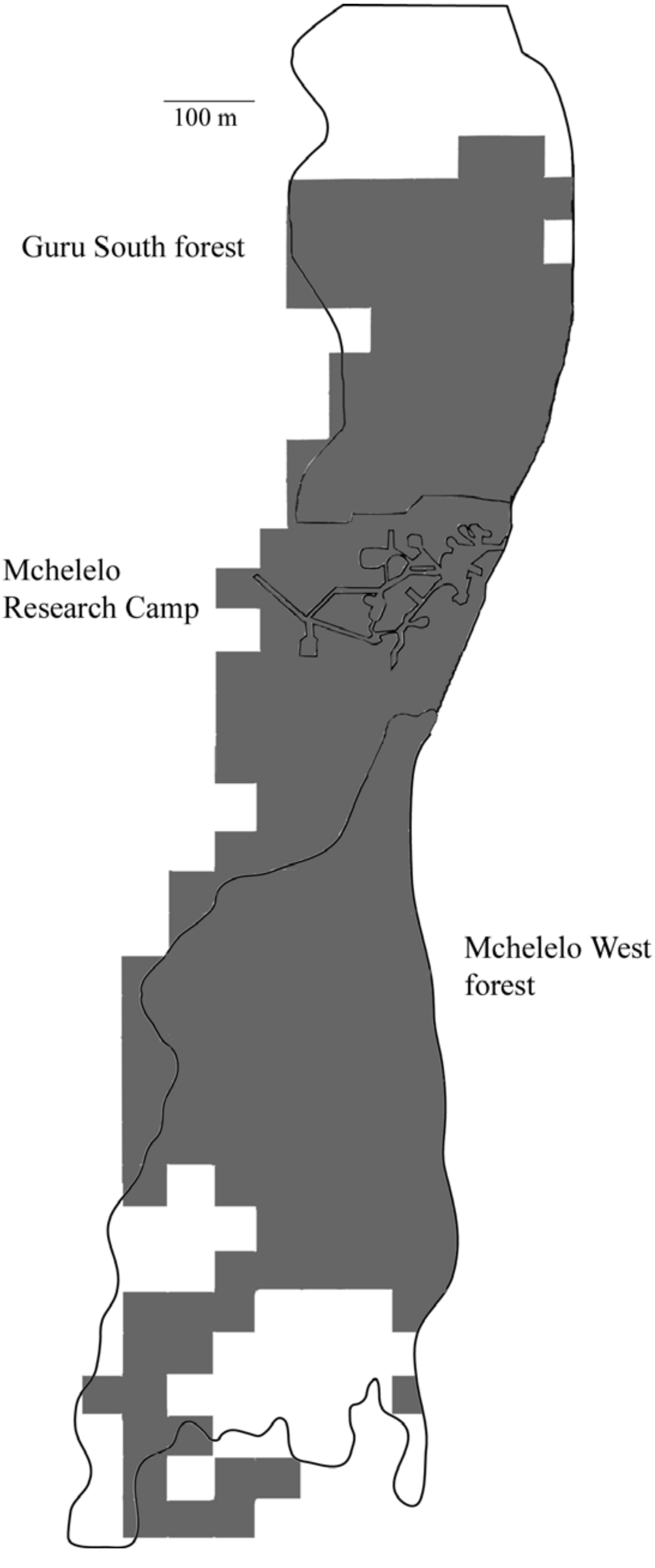

Fig. 4.2. The range of the mangabey group in 2000-01.

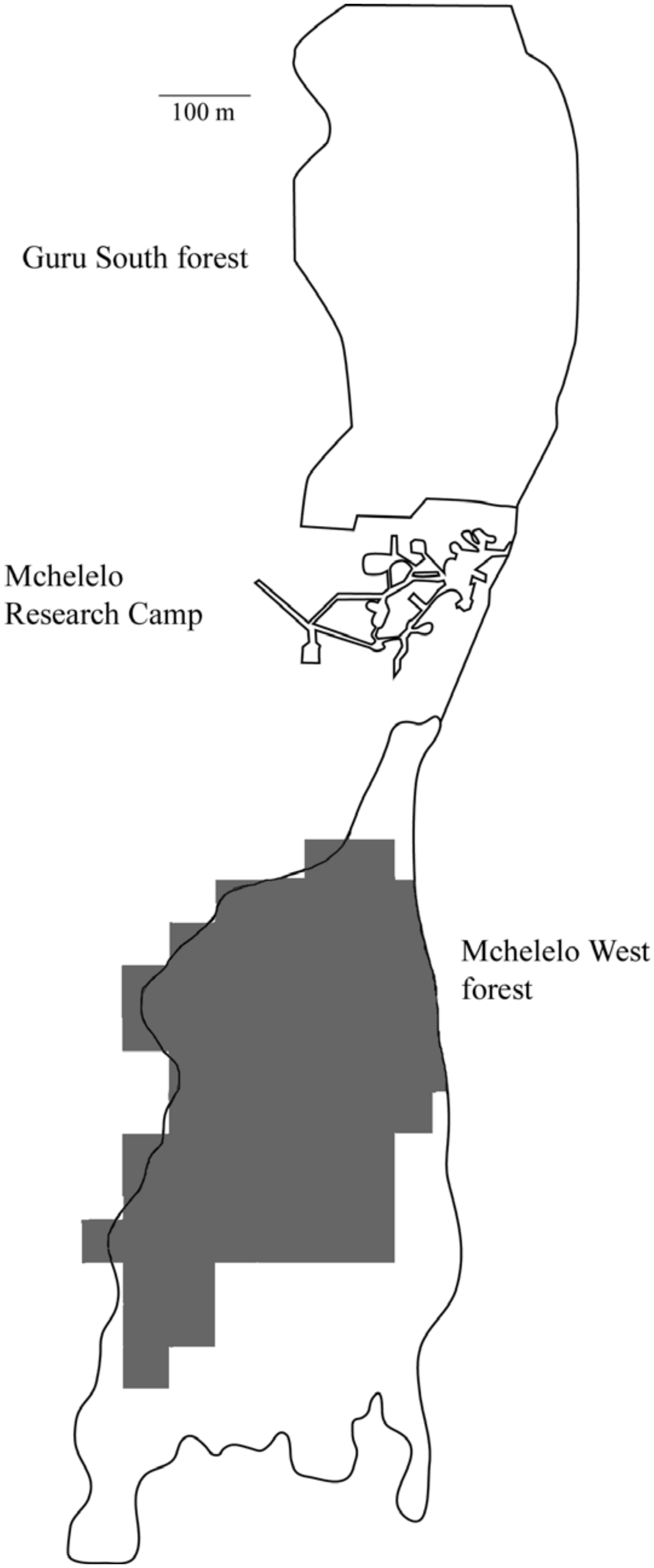

Fig. 4.3. The range of the group in 1988-89. Redrawn from Kinnaird (1990).

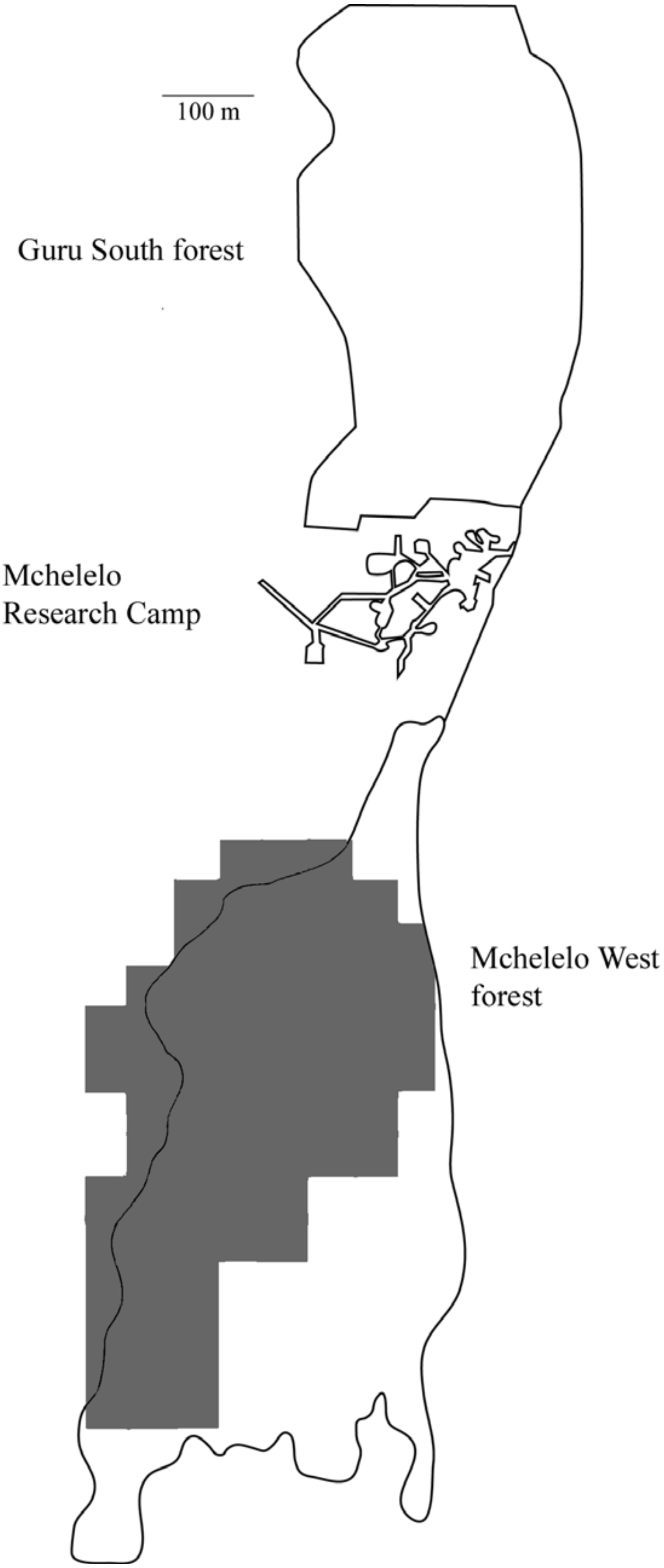

Fig. 4.4. The range of the group in 1974. Redrawn from Homewood (1976).

H2: There was an increase in group size.

The mean size of the Mchelelo West mangabey group in 2000-01 was 50 individuals. The mean group size in 1988-89 was 17 (Kinnaird, 1990) and in 1974 was 36 (Homewood, 1976). The group in 2000-01 was, therefore, the largest of the three groups, and as noted above, had a significantly larger mean daily distance.

H3: There was a decrease in population density.

The population density of mangabeys in Mchelelo West forest in 2000-01 was 1.8 mangabeys per hectare. If the density is calculated for that part of the forest which comprised the study group's range, the value is 1.9 mangabeys/ha. The population density in 1974 was 2.8 mangabeys/ha, whether calculated for the forest or for the home range. The population density in 1988-89 was 1.8 mangabeys/ha within Mchelelo West forest and 1.6 mangabeys/ha within the home range of the study group. The population density in the increased home range of the group in 2000-01 was 1.7 mangabeys/ha.

H4: There was a decrease in food availability in the previous range.

H4a: There was a decrease in density of food trees in the previous range.

The density of reproductively-sized individuals of 23 food species in 16.25 hectares in the current study was 392.61 trees per hectare. The density was 334.83 in 1988-89 (Kinnaird, 1990). These values are not significantly different.

Considering that the group in 2000-01 had 33 more members than in 1988-89, the data were also analyzed as an assessment of whether the abundance of food trees per individual decreased within the previous range. The abundance per individual in

Mchelelo West forest was 320.06 in 1988-89, and 127.60 in 2000-01. This is a significant decrease ($Z = -3.772$; $P < 0.0005$).

Abundance of food trees per individual in the expanded home range of the group in 2000-01 was then analyzed in comparison to the per individual abundance for the group in 1988-89. Abundance of reproductively-sized individuals of the 23 food species was calculated only from those quadrats within the 46.75 hectare range of the group in 2000-01, enumerated from the approximately 50 m by 50 m quadrats in Mchelelo Research Camp and Guru South, as well as Mchelelo West. The abundance of food trees per individual in the increased 2000-01 range was 270.92, which is not significantly different from the value for the group in 1988-89. By increasing its range, the larger group regained access to an equivalent per capita availability of food trees as in 1988-89.

H4b: There was a decrease in fruit availability per hectare in the previous range.

Of the six species whose mean fruit biomass scores (mean monthly fruit score x density x mean DBH) were compared between 1988-89 and 2000-01, four species exhibited significant decreases: *D. mespiliformes* ($t = -4.392$; df = 11; $P = 0.0005$), *F. sycomorus* ($t = -6.137$; df = 11; $P > 0.0005$), *O. spinosa* ($t = -2.381$; df = 11; $P = 0.018$), and *P. reclinata* ($t = -2.223$; df = 11; $P = 0.024$). There was also a significant decrease when all eight species were analyzed together ($Z = -2.762$; $P = 0.003$).

H5: There was an increase in basal area coverage (m^2/tree or m^2/ha/tree) in non-forest corridors.

The mean basal area per tree (m^2/tree) of the non-forest areas that the mangabey group in 2000-01 used to travel between Mchelelo West forest and Mchelelo Research Camp (MCHW-MRC) and to the south of Mchelelo West forest (MCHWTrail10) were 0.051 ± 0.0058 and 0.017 ± 0.0023, respectively. Medley's (1990) Mchelelo North corridor had a mean basal area per tree of 0.073 ± 0.0107, and her Mchelelo South corridor had a mean basal area per tree of 0.215 ± 0.034. A Kruskal-Wallis Test found a significant difference among the four non-forest areas in mean basal area per tree ($\chi^2 = 87.43$; $P < 0.0005$). However, none of the pair-wise comparisons indicated a significant increase. The samples are, in fact, in the wrong direction; the measures in the corridors used by the group in 2000-01 were smaller than those in the corridors not used by the group in 1988-89.

The mean basal area per hectare per tree (m^2/ha/tree) was 0.643 ± 0.0729 for the MCHW-MRC corridor, 0.083 ± 0.0112 for the MCHWTrail10 corridor, 0.552 ± 0.0757 for Medley's (1990) Mchelelo North corridor, and 0.773 ± 0.112 for her Mchelelo South corridor. There was a significant overall difference among the four areas in this measure ($\chi^2 = 103.47$; $P < 0.0005$). None of the pair-wise comparisons, however, indicated a significant increase; the measures had actually decreased. One area through which the group in 2000-01 moved (MCHWTrail10) had a smaller mean basal area per hectare per tree value than either of the areas through which the group in 1988-89 did not move; the other area through which the group in 2000-01 moved (MCHW-MRC) had a smaller value than one of the areas (Mchelelo North) through which the group in 1988-89 did not move.

DISCUSSION

Comparisons between the current study and two earlier studies found an increase in home range to be associated with a decrease in fruit availability per hectare in the previous range and an associated increase in group size for a group of Tana mangabeys. The additional findings of a decrease in abundance of food trees per individual in the previous range, coupled with an equivalent population density in the increased range, and a significant increase in mean daily distance further support the association between an increase in group size and an increase in home range. Other hypothesized associations of the reduced presence of conspecific groups, a decrease in population density in the previous range, an overall decrease in food tree density in the previous range, or an increase in basal area coverage in corridors were not supported.

In the association between group size and home range size, it is generally believed that group size drives home range size; as additional members are added to a group, foraging efficiency decreases and more area is needed to adequately feed all members if food abundance is constant (e.g., Takasaki, 1981, 1984; Terborgh, 1983; Terborgh and Janson, 1986; Di Bitetti, 2001). It should be noted, however, that in the comparisons presented here, there is no association between a larger home range and a larger group size when comparisons are made between 1974 and 1988-89; the association between increased group size and increased home range is only in terms of the group in 2000-01. The group was half the size in 1988-89 that it was in 1974, yet had a slightly larger home range by 1.75 hectares. As a consequence, there was a decrease in population density between 1974 and 1988-89 in Mchelelo West forest, and the decreased density persists today. What occurred between 1974 and 1988-89 to cause a substantial decrease in group size and population density?

Decker and Kinnaird (1992) found a significant decline in the number of mangabey groups per forest in 23 forests surveyed in 1974 and in 1987. There was no significant change observed in mean group size; the groups were not forming 'super-groups' (Homewood, 1976). Neither a disease epidemic nor a drought, hypothesized reasons for the decline, were supported (Marsh, 1986). Instead, the decline in the mangabey population may have been caused by forest senescence (lack of regeneration) that occurred in several forests during the same time period (Marsh, 1986; Medley, 1990), and/or loss of forest area to clearance for farmland and to river course changes that occurred since the early 1960's (Decker, 1989; Medley, 1990). These changes reduced the ability of the forests to support primates, either because of a declining resource base or decreased forest area. Decker (1989) argues that the densities of both the mangabey and the red colobus were very high in the 1970's because the groups had been compressed into smaller forest areas by forest destruction, and hence were above carrying capacity. The fact that the population density in Mchelelo West forest in 1988-89 and in 2000-01 were both 1.8 mangabeys per hectare, in addition to the finding that the population density in the increased home range of the group in 2000-01 was a very similar 1.7 mangabeys per hectare, also supports this argument that the higher population density in 1974 was due to crowding. High densities in small or fragmented forests, as compared to large or intact forests, have also been found in *Alouatta pigra* by Ostro et al.

(1999) in Belize and Estrada et al. (2002) in Mexico, and compression into refugia created by clearance for farmland may be responsible for high primate densities within certain forests in Kibale National Park, Uganda (Chapman and Lambert, 2000). Similarly, Granjon et al. (1996) measured a significantly higher mean abundance per kilometer of eleven monkeys and large terrestrial mammals in French Guiana after flooding reduced available land, presumably because the animals were crowding onto the non-flooded land. The significant decline in Tana River population numbers between 1974 and 1987 may therefore have been due to the primates responding to the smaller forest areas, declining to the carrying capacity (Decker, 1989).

Mchelelo West forest suffered forest loss to farmland in the 1960's. In 1966, a 12 hectare area to the north was cleared and farmed until 1969; in 1969, a 16 hectare area to the south was cleared and farmed until 1973 (Marsh, 1978). These farms, even after abandonment, served to separate Mchelelo West forest and the primate groups within it from Guru South forest to the north and the Congolani forests to the south. What had been part of a 172 hectare forest (Decker, 1994) was a bounded 17 hectares in 1974 (Homewood, 1976). The fact that this forest clearance impacted the mangabeys just as much as the arboreal red colobus is evident in the fact that Homewood (1976) and Kinnaird (1990) did not observe the Mchelelo West mangabey group ranging outside the forest boundaries. The smaller group size and density in 1988-89 may have been due to the limited space and foraging area the group found themselves in after 1969, declining after the initial compression following severe forest loss.

The mangabey group in 1988-89 was once observed, however, to move through non-forest habitat between Mchelelo West forest and Mchelelo Research Camp. The group followed an old female, and moved through bushes along the riverbank, turning back to Mchelelo West forest only when they heard a radio playing in camp (M. Kinnaird, pers. comm.). Soon after Kinnaird's study ended, the group began to regularly travel through Mchelelo Research Camp and to Guru South forest (G. Galana, Kinnaird's field assistant, pers. comm.). With these additional observations, it appears possible that the home range expansion occurred before the group size increased and may have initially been due to less hesitation of crossing through non-forested habitat, especially the research camp (M. Kinnaird, pers. comm.). This ability to travel through non-forested habitat is part of the mangabey's behavioral flexibility, and may prove critical to its survival.

Considering that there was no decrease in habitat quality in Mchelelo West forest between 1974 and 1988-89, as measured either by density of food trees (Decker, 1989) or fruit abundance (Wieczkowski, in prep. b), which might have caused the mangabey group to expand its range, it appears possible that soon after Kinnaird's (1990) study the group began to simply regain the range it occupied before forest destruction isolated Mchelelo West forest. The other Tana mangabey groups that have been studied occupied larger home ranges than those occupied by the Mchelelo West groups in 1974 and the 1988-89: 20 hectares (Nkano group, Kinnaird, 1990); 52.75 hectares (Mnazini North group, Homewood, 1974); and 70 hectares (South Mchelelo group, Kinnaird, 1990). As these groups contained 16, 17, and 28 individuals, respectively, the larger home ranges are not solely a consequence of larger groups. This regaining of range size may be similar to observations of a group of *Alouatta palliata* in Costa Rica which lost access to part of their home range due to deforestation. Within three years, the group had regained some area back by expanding their home range in a new direction (Clarke et al., 2002).

It is not clear why the Mchelelo West mangabey group has increased to such a large group size, although mean group size throughout the mangabeys' distribution has also increased since earlier studies. Wieczkowski and Mbora (2002) reported a mean group size of 30.4 (n = 17 groups). This compares to a mean group size of 20.5 in 1988-89 (Kinnaird and O'Brien, 1991; n = 7) and 26.5 in 1973-74 (Homewood, 1976; n = 4). Unfortunately, only three or four groups were counted in common between any two studies, and only two counts are accompanied by any type of ecological data from the groups' ranges.

Because feeding competition is more intense in larger groups than smaller groups if food abundance is constant, the per capita foraging efficiency is lower in larger than smaller groups (Terborgh and Janson, 1986). A larger group, therefore, will need to travel over more space in order to gain adequate per capita resources (Terborgh, 1983). By increasing home range size and daily distance, the 50 mangabeys of the Mchelelo West group in 2000-01 have access to a greater number of food trees and an equal per capita abundance of food trees as the 17 mangabeys of the group in 1988-89 had in the previous range. In addition, because the group's increased home range size incorporates other forested areas, overall population density in Mchelelo West forest has remained stable despite the increase in group size.

Wieczkowski (in prep. a) found that forest area, as well as density of trees ≥ 10 cm DBH, were significantly positively associated with the mean number of mangabey groups per forest in 31 study forests. The finding of that study, along with the preceding discussion of the impact forest loss can have on the demography and behavior of a single group, emphasizes the importance of forest area to the Tana mangabey. Unfortunately, 30% of the minimum total area of forest that was present along the lower Tana River in 1994 has been cleared (Wieczkowski and Mbora, 1999-2000). Protecting forest cover clearly should be of priority in management of the Tana River area, and the national moratorium on clearance of indigenous forest must be enforced. A solution must also be found, with the full cooperation of the local people affected, to forest loss to farmland within the Tana River Primate National Reserve, and forest restoration should be undertaken to replace forest already lost, especially in corridors between neighboring forest patches.

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CHAPTER 5

CONCLUSION

Although the three manuscripts in this dissertation are independent, together they form a multifaceted examination of the Tana mangabey's use of a fragmented and diverse habitat, within the context of its ecological flexibility. In this final chapter, I will discuss this unified body of research, its contributions to primate literature, and how it might inform management and conservation in the lower Tana River.

Despite its endemism in riverine forest fragments along 60 kilometers of the lower Tana River, Kenya, the mangabey appears to be very general in its habitat needs. Although several hypotheses that were derived from previous studies on the mangabey were examined, mangabey abundance in forest fragments was found to be influenced primarily by forest area, and secondarily by the density of sub-canopy and canopy trees. This apparent lack of specific habitat needs allows the mangabey to persist in approximately 40 of the 62 fragments [Butynski and Mwangi, 1994; Mugo, 1996; pers. obs.], in spite of the dynamic and variable nature of those fragments.

The current study was similar to three others that found forest size to positively impact abundance or presence of primates [Estrada & Coates-Estrada, 1996; Lawes et al., 2000; Umapathy & Kumar, 2000b], but differed from Onderdonk and Chapman [2000], who did not find a relationship between size and primate presence. It is interesting to note that the four studies to find forest size important included larger forests and wider ranges of forest sizes [4.8-408 ha: this study; 2-1,000 ha: Estrada & Coates-Estrada, 1996; ¼-1,732 ha: Lawes et al., 2000; 1-2,500: Umapathy and Kumar, 2000b] than the one that did not find an association with forest area [1-130 ha: Onderdonk and Chapman, 2000].

In addition to their general habitat needs, the mangabeys' ecological flexibility may also aid their survival in this highly diverse and fragmented system. One of the more critical aspects of this flexibility is their ability to move between forest fragments, including their capability of traveling through non-forest habitat. The mangabeys are able to compensate for a lower per capita abundance of food trees by including neighboring forests in their home range. Although this was studied in the context of a group that had increased in size, it may also serve the mangabey in situations when there are natural or anthropogenic declines in food abundance. For example, there are numerous forests in the eastern half of the TRPNR that have undergone extensive forest clearance and human forest product use [Wieczkowski & Mbora, 1999-2000]. Several of the mangabey groups inhabiting that area move between two forests, even traveling through one kilometer of non-forest to reach a neighboring forest [pers. obs.]. Further investigations should be undertaken to determine what ecological conditions influence their movement and what behavioral changes result from their use of more than one forest.

Contrary to existing characterizations, the mangabeys are not ripe fruit specialists. Instead, for a number of their important diet species, they consume ripe fruit, ripe seed, unripe fruit, and/or unripe seed in positive correlation with availability. In view of the seasonality of overall fruit production and the various fruiting schedules of individual species [Homewood, 1976; Kinnaird, 1990], this lack of specificity for any one diet item may allow the mangabey to consume adequate resources throughout the year. Their lack of specialization ameliorates the effects of seasonality of fruit production and associated periods of potential resource scarcity.

By studying primates over longer temporal and additional spatial scales, researchers are beginning to recognize dietary variability within species [e.g., Chapman, 1987; Chapman et al., 2002] or between related species [e.g., Goldsmith, 1999; Kaplin & Moermond, 2000], and even to re-think the dietary categories in which primates have been placed [e.g., *Colobus polykomos*: Dasilva, 1994]. This dissertation offers evidence for redefining the dietary category to which the Tana mangabey belongs. This species has been considered to be primarily a frugivore, which can switch to a diet of seeds when productivity of the habitat declines. My findings of a continued reliance on seeds (since the study by Kinnaird (1990) of the group in 1988-89) suggest that a diet dominated by seeds may be more typical of this mangabey.

Another important contribution of this dissertation is to the understanding of dietary choice in the genus *Cercocebus*. Although there is dental morphology evidence that *Cercocebus* mangabeys are adapted to subsisting on hard nuts and seeds [Fleagle & McGraw, 2002], there are few studies that have investigated feeding ecology. Some of these did not distinguish between fruit and seeds [e.g., *C. atys*: Fimbel, 1994a; *C. torquatus*: Mitani, 1989], further limiting the conclusions that can be made about *Cercocebus* diet. My findings, in addition to Kinnaird's [1990], provide dietary support to the morphological evidence that *Cercocebus* is a seed eater.

There is also evidence of the mangabeys' flexibility in choice of diet species. Plants that had been previously considered "critical" diet species, *Phoenix reclinata* and

Ficus sycomorus, were not found to influence mangabey abundance in forest fragments throughout the mangabeys' 60-km distribution. The dietary data support the importance of these species where they do occur; the lack of a relationship is due to their absence from many occupied forests, and therefore from the mangabeys' diet in those forests. In addition, the number of groups was correlated with the mangabey's important diet species only within the TRPNR, where all of the dietary studies to this point in time have been undertaken. These results suggest that it would be informative to conduct behavioral studies in additional forests outside the TRPNR. Considering the extensive floral diversity found throughout the lower Tana River [Medley, 1992], and given the current evidence of the mangabey's ecological flexibility, it would not be unanticipated if we found the mangabeys consuming additional diet species, beyond those documented to date, in these unstudied forests. Findings with other primate species verifying that composition and density differences may result in dietary variation between populations [Chapman & Fedigan, 1990; Chapman et al., 2002; Swedell, 2002] further indicate that such expansion of research would be worthwhile in fully assessing the mangabeys' dietary flexibility.

Despite their general habitat needs and the various aspects of ecological flexibility that have now been further documented, the Tana mangabey is considered one of the world's most endangered primates [Mittermeier & Konstant, 2002]. This classification is due to the combination of limited forest habitat and extreme forest loss and degradation. With only 2,616 ha of forest estimated in 1994 [Butynski & Mwangi, 1994], the consequences of these human activities (i.e., reduced forest area, and loss of structural and diet resources) can be devastating. The recent destruction of the 500 ha Nkanjonja forest, just north of the TRPNR on the east bank, reduced the amount of forest area in the lower Tana River by 19% [Wieczkowski & Mbora, 1999-2000]. This one forest was known to support 8% of the total mangabey population [Butynski & Mwangi, 1994]. Forest loss and degradation have impacted mangabey behavior, as well. Prior to the current fieldwork, there had been no observations of mangabeys crop raiding; due to the planting of crops on cleared forest land in Makere East in 1999, one of the groups there began to raid crops [pers. obs.].

It also appears that the impact of human activity goes beyond these consequences. The higher level of human activity outside the TRPNR is hypothesized to be significant enough to even override possible correlations between mangabey abundance and forest structural attributes. The impact on the mangabeys clearly goes beyond the resources actually harvested and is further exemplified by Wieczkowski and Mbora's [1999-2000] observations of mangabeys being chased by dogs in several forests. While trying to count the mangabey group in Guru East forest, I witnessed the group's behavior change markedly (e.g., fewer vocalizations, faster movement, less stationary activity) after they had been chased by dogs.

In addition to the goal of studying the Tana mangabey's habitat use and ecological flexibility, an aim of this dissertation was to apply the results to inform management and conservation of this critically endangered primate. The specific contributions have been discussed in the individual manuscripts. Here, there are three general areas of application that can be mentioned.

First, the forests of the lower Tana River should be managed for forest area, density of sub-canopy and canopy trees, and coverage of at least the mangabeys' major diet species documented to date. Although the mangabeys can cross through non-forest habitat to reach neighboring forests, they have not been observed to travel far over completely open ground. Management should therefore also focus on maintaining plant cover between forest fragments to allow mangabey movement between them.

Second, the extended temporal investigation of the mangabeys' ecological flexibility suggests that additional study is warranted before making final management recommendations. Although the three dissertations that have studied the Tana mangabey have found a large amount of ecological flexibility – in behavior, diet, ranging, intergroup encounters, and grouping – they have all been undertaken in just three forests, all on the west bank of the TRPNR. The contribution that behavioral studies can make to conservation is information on the range of behavioral and ecological responses a species is capable of across the habitat diversity in which they are found [e.g., Tutin, 1999; Fleury & Gautier-Hion, 1999]. Knowledge of limitations to those responses is just as critical. The forests of the lower Tana River are incredibly diverse in their species composition, forest structure, and level of human impact. By restricting our study of the mangabeys' ecological flexibility to a few forests, we are potentially failing to observe the full range and limitations of that flexibility. Research should now expand into more forests, to increase the habitat diversity in which we observe this species' behavior and ecology, and to more fully understand their responses to anthropogenic habitat change. Although we might predict that the mangabey could potentially use secondary forest re-growth, or perhaps pioneer species post-disturbance, as some primates can [e.g., *Sagiunus midas*: Rylands & Keuroghlian, 1988; Schwarzkopf & Rylands, 1989; *Cercopithecus ascanius*, *C. mitis*, *C. pogonias*, and *Colobus guereza*: Thomas, 1991; *Cercopithecus* *campbelli*, *C. petaurista*, *Cercocebus atys*, and *Pan troglodytes*: Fimbel, 1994b], this remains to be determined.

Third, recent forest loss and degradation in the lower Tana River [Wieczkowski & Mbora, 1999-2000] are a clear sign of failed biodiversity management and conservation. Much of this forest destruction was a reaction by the Tana River human communities when they felt threatened by outside management, especially in relation to the disastrous World Bank-funded Tana Global Environmental Facility (GEF) project [Mbora, 2000b]. Research on the human population is certainly called for, with the aim of assessing the potential success or failure of community-based conservation and education programs, as well as revived traditional forms of management. If the local people are included in management of their forest resources, they may feel less alienated from and more invested in those resources. If they are excluded, then forest loss and degradation will very likely continue. For the highly endangered primates of the Tana area, continuation of ill-informed policies in relation to the local human population will prove as detrimental as inadequate management of forests resulting from deficiencies in ecological data.

This dissertation raised as many questions as it answered. Although the information that we have obtained from each of the studies undertaken on the mangabey is a solid base from which to further investigate this species' behavioral and ecological adaptations to its dynamic and fragmented habitat, the ongoing research continues to suggest new avenues. Investigation of the mangabeys' seed diet would be greatly enhanced by nutritional analyses, as well as identification of any biological features (e.g., physiology of digestion) that allow a concentration on this diet item. The role the mangabey plays in forest dynamics (e.g., seed dispersal and predation, regeneration in non-forest corridors) should also be assessed. Finally, as mentioned throughout this dissertation, research should include more of the habitat diversity present in the lower Tana River. By further expansion of study we may ultimately understand the full behavioral and ecological repertoire of the Tana mangabey, and very importantly, the limits to that repertoire that will limit the survival of this endangered primate.

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