

RESEARCH ARTICLE

Shifting Forest Composition and Primate Diets: A 13-Year Comparison of the Tana River Mangabey and its Habitat

JULIE WIECZKOWSKI^{1*} AND MARGARET KINNAIRD²¹Department of Anthropology, University of West Georgia, Carrollton, Georgia²Mpala Research Centre, Nanyuki, Kenya and Wildlife Conservation Society—International Programs

We compared the feeding behavior of a group of Tana River mangabeys (*Cercocebus galeritus*), densities of 25 diet species, and fruit availability of nine species in a 16.25 ha Tana River forest in southeastern Kenya studied in 1988 and in 2000–2001. For both studies, we enumerated all reproductively sized individuals of the 25 diet species and sampled nine of those species monthly for fruit availability. Mangabey feeding data were collected monthly from January to December 1988 and August 2000 to July 2001 using identical methods. We found a 17% increase in stem number of the 25 species between studies. Estimates of fruit production were lower in 2000 for five of the nine species monitored. Species composition of the mangabey diets shifted between 1988 and 2000–2001. We suggest that changes in forest composition may be due to declining human disturbance, elephant loss, changes in the river's hydrologic regime, and the 1997/98 ENSO event. Possible reasons for lower fruit availability are a younger demographic profile of the forest and changes in the river's hydrological regime. Only some of the changes in the mangabey diet mirrored changes in stem abundance and/or fruit availability. Mangabey dietary changes underscore their high degree of flexibility that allows them to persist in such a dynamic forest habitat. *Am. J. Primatol.* 70:339–348, 2008. © 2007 Wiley-Liss, Inc.

Key words: *Cercocebus*; temporal comparison; diet; forest composition; habitat change; fruit phenology

INTRODUCTION

Tropical forests are highly dynamic over space and time owing to shifts in plant species composition, density, and phenological phases of fruiting and flowering [Chapman et al., 1997; Condit et al., 1992; Fashing et al., 2004; Newstrom et al., 1994]. In addition to the vagaries of natural disturbances, tropical forests are modified, fragmented, and eliminated by human activities. Animal populations that rely on naturally dynamic or anthropogenically altered forest habitats may respond to changes by migrating, shifting home ranges, or altering diet or activity budgets [Leighton & Leighton, 1982; Kinnaird, 1990; Olupot et al., 1994; Tutin, 1999; Clarke et al., 2002]. Among primates, dietary flexibility has been shown to play an important role in a species' ability to adapt to and survive in dynamic or altered habitats [Estrada et al., 1999; Olupot, 1998; Rodríguez-Luna et al., 2003; Singh et al., 2001]. For example, the white-handed gibbon (*Hylobates lar*) and the banded leaf monkey (*Presbytis melalophos*) remain on territory after preferred fruit trees are eliminated by selective logging, but they compensate by increasing their intake of foliage [Johns, 1986]. In contrast, Sumatran orangutans (*Pongo pygmaeus abelii*) follow differences in ripe fruit availability

across altitudinal zones by moving across those zones on a seasonal basis [Buij et al., 2002].

Nevertheless, current levels of forest loss, fragmentation, and modification are often too great and too rapid for adequate response by many primate species, even those showing generous degrees of behavioral plasticity. Understanding the variability and limitations of primate responses to natural and anthropogenic habitat change is critical if we are to efficiently and effectively focus our conservation actions [Fleury & Gautier-Hion, 1999; Tutin, 1999].

The Tana River system in southeastern Kenya is particularly appropriate for addressing questions of how animals respond to natural and anthropogenic

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

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influences on their habitats. Because Tana River forests are dependent on ground water and periodic flooding for their persistence, they are spatially restricted (approximately 2300 ha). In addition, the forests are variable in shape and size, their plant communities are highly dynamic and heterogeneous [Hughes, 1988, 1990], and they exhibit interannual variation in leafing and fruiting patterns [Kinnaird, 1992b; Marsh, 1978b]. Humans are converting forests for farmland and removing forest products (e.g., building materials, food and drink) [Wieczkowski & Mbora, 2000], many of which are important primate foods [Kahumbu, 1992; Kinnaird, 1992a; Medley, 1993]. The endemic Tana River mangabey (*Cercocebus galeritus*) responds to the spatial and temporal changes in its habitat through behavioral and ecological flexibility in feeding, ranging, intergroup interactions, and grouping [Homewood, 1976; Kinnaird, 1990; Wieczkowski, 2005]. For example, mangabey groups merge together when their fruit resources are abundant and uniformly distributed, engage in aggressive encounters when resources are abundant and clumped, and avoid one another when resources are scarce [Kinnaird, 1992c]. However, the extent of this flexibility is not clear. The species is currently listed by the World Conservation Union [IUCN, 2006] as Critically Endangered owing to its limited distribution and the extreme loss and degradation of its habitat [Wieczkowski & Mbora, 2000].

We conducted two year-long studies of Tana River forests and Tana River mangabeys in 1988 and 2000–2001. Both studies examined how mangabey feeding ecology is influenced by forest composition and patterns of fruit production. We did not attempt to distinguish between the effects of anthropogenic change and natural habitat change on the mangabeys, but rather investigated how they respond to overall habitat changes. Because the degree and nature of their responses to the natural dynamics of the Tana River forests (e.g., seasonal availability of food, forest loss and gain because of river course changes) is critical to adaptation to anthropogenic changes (e.g., forest clearing, degradation, and fragmentation), an understanding of how mangabeys respond to any habitat change will ultimately aid the management of their populations and habitat.

We took advantage of the fact that data in both studies were collected in similar ways for the same mangabey group in the same forest patch to pose two hypotheses concerning mangabey responses to the variability that characterizes their forest habitat: (1) the study forest underwent significant changes in forest composition and fruit production between 1988 and 2000–2001; and (2) mangabeys responded to these changes by shifting their diets to mirror the changes in species composition and fruit production.

METHODS

Study Area

We conducted our studies within the Tana River Primate National Reserve (TRPNR) in southeastern Kenya (1°45′–2°00′ S, 40°07′ E; Fig. 1). The TRPNR is considered semi-arid with a mean annual rainfall measuring less than 500 mm, and mean daytime temperatures ranging from 30 to 38°C [Butynski & Mwangi, 1994]. The riverine forests that border the lower Tana River are dependent on the height of the groundwater table and the river's processes of inundation, nutrient recharge, and erosion [Hughes, 1988]. The forests are naturally fragmented owing to the meandering nature of the river; however, clearing for agriculture exacerbates fragmentation and contributes to significant forest loss. In 15 years before being gazetted as a primate reserve (1960–1975), forest area declined by 56% and fragmentation increased dramatically [Medley, 1990]. After the TRPNR was gazetted in 1976, forest loss declined, measuring only 4% between 1975 and 1987 [Medley, 1990]. Forest destruction and loss escalated again in the late 1990s: a minimum of 30% of forest in the lower Tana River was lost and one 500-ha fragment was almost completely felled [Wieczkowski & Mbora, 2000].

Our study forest, Mchelelo West, is an active levee evergreen forest found on sandy soils [Hughes, 1988]. The forest is above annual flood level, experiencing floods every 5–25 years. Of all forest types of the lower Tana River, active levee evergreen forest has the most diverse plant species composition [Hughes, 1988]. The canopy is closed at 10–20 m with emergents to 30 m. The river borders the forest on the east and the forest's western edge is determined by the depth of the groundwater table. Before the 1960s, Mchelelo West was part of a continuous 172 ha forest, but in the 1960s and 1970s a 12 ha area to the north of and a 16-ha area to the south of Mchelelo West were cleared, farmed, and abandoned [Marsh, 1978a]. These areas had not regenerated by our first study but were beginning to recover by our second study. Mchelelo West forest measured 17 ha in 1988 and 26 ha in 2000–2001 [Kinnaird, 1990; Wieczkowski, 2005]; although the forest increased in size owing to an increase in tree cover on the abandoned farmland, it did not regain continuity with forests to the north or south. A system of clearly marked quadrats of 0.25 ha was in place during both studies.

Study Group

We studied the Mchelelo West mangabey group from January to December 1988 and August 2000–July 2001. Local field assistants who had contact with the group from 1987 through 2001 identified the 1988 and 2000–2001 study groups as

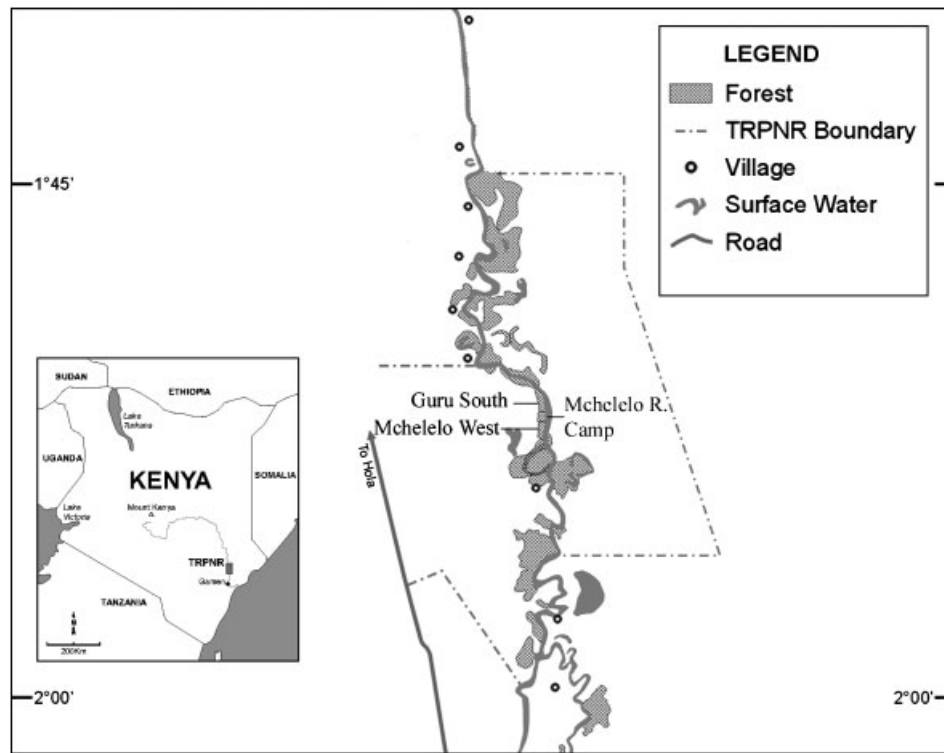


Fig. 1. The Tana River Primate National Reserve (TRPNR), with study forests highlighted. Adapted from Wiczkowski [2005].

the same group, and confirmed that the group had increased in size through births and immigrations [Galana & Galana, personal communication]. During 1988, the group included 17 individuals and ranged within 18.75 ha that included the Mchelelo West forest and adjacent non-forest areas [Kinnaird, 1990]. In 2000–2001, the group numbered 50 individuals and ranged over 46.75 ha, covering Mchelelo West forest, and the Mchelelo Research Camp and Guru forest to the north (Fig. 1) [Wiczkowski, 2005].

As the research presented in this study was conducted on nonhuman primates in their natural habitat, we were not required to be approved by an Institutional Animal Care and Use Committee. We confirm that all research reported here adhered to the legal requirements of Kenya.

Data Collection

Vegetation

Twenty-four canopy and sub-canopy trees and one liana species were selected to characterize vegetation and measure food availability (Table I). Species were initially chosen in 1988 based on their importance to the mangabey diet. We enumerated all reproductively sized individuals of these species in the same 16.25 ha of Mchelelo West forest in 1988 and in 2000–2001.

Nine of the 25 plant species (Table I) used to characterize vegetation were monitored for phenological activity on the day immediately before or subsequent to each 3-day follow of the mangabeys (see below). These nine species were selected because of their importance to the mangabey diet; they contributed from 66.4 to 76.6% of the annual diet of mangabey groups studied in Mchelelo West forest [Homewood, 1976; Kinnaird, 1990; Wiczkowski, unpublished data]. The more common species were represented by at least ten individuals (range of n per species = 10–13); for species whose populations did not include ten individuals, all individuals present were monitored (range of n per species = 8–9). We did not attempt to monitor the same individuals in 1988 and in 2000–2001 owing to loss of tree tags, death of some individuals, and the high abundance of some species. The presence of unripe and ripe fruits was scored on a 0–5 scale measuring the proportion of the total canopy covered (0 = 0%, 1 = 1–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%). We measured each tree's diameter at breast height (DBH) and calculated a mean for each species. Because DBH is an accurate estimate of fruit number and/or biomass [Chapman et al., 1992; McDiarmid et al., 1977], we multiplied a species' mean fruit score by its mean DBH to convert our fruit scores to estimates of tree fruit crop. We then multiplied this tree fruit crop by the

TABLE I. The 25 Species Enumerated

Taxon	Life form	Pioneer or late succession?	Phenology tree?
Alangiaceae			
<i>Alangium salviifolium</i>	Canopy tree	Late succession ^f	Yes
Anacardiaceae			
<i>Lannea schweinfurthii</i> ^a	Canopy tree	Pioneer ^h	
<i>Sorindea madagascariensis</i>	Canopy tree	Late succession ^c	Yes
Apocynaceae			
<i>Rauvolfia mombasiana</i>	Subcanopy tree		
<i>Saba comorensis</i>	Liana		
Boraginaceae			
<i>Cordia goetzei</i>	Canopy tree	Late succession ⁱ	
Caesalpinaceae			
<i>Cynometra lukei</i> ^b	Canopy tree		
<i>Tamarindus indica</i>	Canopy tree		
Ebenaceae			
<i>Diospyros mespiliformes</i>	Canopy tree	Late succession ^c	Yes
Flacourtiaceae			
<i>Oncoba spinosa</i>	Subcanopy tree	Late succession ^d	Yes
Guttiferae			
<i>Garcinia livingstonei</i>	Canopy tree	Pioneer ^e	
Mimosaceae			
<i>Acacia robusta</i>	Canopy tree	Pioneer ^g	Yes
<i>Albizia glaberrima</i>	Canopy tree	Pioneer ^j	
<i>Albizia gummifera</i>	Canopy tree	Pioneer ^c	
Moraceae			
<i>Ficus bubu</i>	Canopy tree		
<i>F. bussei</i>	Canopy tree		
<i>F. natalensis</i>	Canopy tree		
<i>F. sycomorus</i>	Canopy tree	Pioneer ^g	Yes
Palmae			
<i>Hyphaenae compressa</i>	Canopy tree	Pioneer ^k	Yes
<i>Phoenix reclinata</i>	Subcanopy tree		Yes
Sapindaceae			
<i>Aporrhiza paniculata</i>	Canopy tree		
<i>Blighia unijugata</i>	Canopy tree	Late succession ^c	
Sapotaceae			
<i>Mimusops fruticosa</i>	Canopy tree		Yes
<i>Pachystela msolo</i>	Canopy tree	Late succession ^c	
Sterculiaceae			
<i>Sterculia appendiculata</i>	Canopy tree	Late succession ^c	

^a*Lannea stuhlmannii* in Kinnaird [1990] [Beentje, 1994].

^b*Cynometra webberi* in Kinnaird [1990] [Beentje, 1994].

^cMarsh [1986].

^dLwanga [2003].

^eDecker [1989].

^fMedley [1994].

^gMedley [1990].

^hBloesch and Klötzli [2004].

ⁱWelch [1960].

^jSheil et al. [2000].

^kStave et al. [2003].

species' density to derive an estimate of a species' forestwide fruit crop.

Mangabey diets

We collected mangabey behavioral data from 0700 to 1815 in one block of 3 days per month from January to December 1988 and August 2000 to July 2001. Every half an hour, we spent 10 min scanning the group and recorded for each visible

individual, its location and the first behavior sustained for 5 sec [Altmann, 1974]. The two behaviors of interest for this study are "eat" and "forage". "Eat" is defined as an animal chewing or ingesting a food item, either directly from the habitat or from its cheek pouches. Animals eating while engaging in any other activity were scored as eating. "Forage" is 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. If an individual was eating or foraging from the habitat, we also recorded the plant species. Because the group ranged over a smaller area in 1988 (18.75 ha) than in 2000–2001 (46.75 ha), we sub-sampled the 2000–2001 data and considered only those data gathered while the group was in the 1988 range. In 2000–2001, the group spent 53% of its time (217 hr) in this smaller area. Of the 36 days of observation in 2000–2001, there were only 2 days (1 in August and 1 in April) when the group did not spend time in the 18.75 ha.

Data Analysis

We used Wilcoxon signed-rank tests to test for differences in diet trees in our 1988 and 2000–2001 vegetation samples, and to test for differences in the mangabey diets between 1988 and 2000–2001. For the latter, we analyzed the number of eating and foraging events on each of the 25 diet species and other diet items grouped together as “other minor species”. The tests were two-tailed with a *P*-value of 0.05. We calculated diet overlap between 1988 and 2000–2001 using Schoener’s overlap index [Krebs, 1999], and included all species scored during “forage” or “eat” events. Schoener’s overlap index is calculated as:

$$P_{jk} = \left[\sum_{i=1}^n (\min p_{ij}, p_{ik}) \right] 100$$

where P_{jk} is percentage overlap between the group’s diet in 1988 and in 2000–2001; p_{ij} , proportion species i is of the total resources used by the group in 1988; p_{ik} , proportion species i is of the total resources used by the group in 2000–2001; n , total number of species.

In addition, we calculated a selection index for each of the 25 species for the two studies as the proportion of species i in the diet divided by the proportion of species i in the environment [Krebs, 1999]. An index greater than 1 shows preference for that species, whereas an index less than 1 shows no preference.

RESULTS

Vegetation

We measured a 17% increase between 1988 and 2000–2001 in the number of stems represented by the 25 diet species ($n = 5452_{1988}, 6398_{2000}$; Table II). Numbers of stems per species differed significantly between the two periods ($Z = -2.092$; $P = 0.036$). Nine of the 11 (there was a tie for tenth place) most abundant species in 1988 were also the most abundant in 2000–2001. The majority of species that were the most abundant in both studies are late succession species (Tables I and II). One pioneer species, *Garcinia livingstonei*, dropped out of the top

ten, whereas another, *Acacia robusta*, was added. Two others, *Hyphaene compressa* and *Albizia gummifera*, remained in the top ten. These pioneer species tend to be distributed in quadrats bordering the edge of the forest (*A. robusta*: 59%; *A. gummifera*: 25%; *H. compressa*: 55%).

Seven of the nine species monitored for fruiting differed in estimates of fruit production between 1988 and 2000–2001 (Fig. 2). *A. robusta* and *H. compressa* had higher fruit scores, whereas *Alangium salviifolium*, *Diospyros mespiliformes*, *Ficus sycomorus*, and *Phoenix reclinata* had lower fruit scores in 2000–2001. *Mimusops fruticosa* did not fruit at all in 2000–2001. Although all of the species included in the phenological sample increased in stem abundance between 1988 and 2000–2001, mean DBH decreased for the seven non-palm species (Table II). The lower phenological scores were, therefore, due to lower mean fruit scores and/or smaller mean DBHs in 2000–2001. In addition, the fruit crop of the nine species added together was lower in 2000–2001, almost entirely owing to the lower *P. reclinata* fruit crop (Fig. 2).

Mangabey Diets

Twenty-three of our 25 selected diet species comprised 89.3% of the group’s diet in 1988 and 82.9% of the diet in 2000–2001 (Table II). The remaining two species, *Albizia glaberrima* and *Ficus bussei*, were not consumed during either time period. Schoener’s diet overlap between the two time periods measured for all plant species was 59.7. In 1988, the group ate 36 species, 13 of which were not eaten in 2000–2001. These 13 contributed 18.7% of the diet. In the group 2000–2001 ate 33 species. Ten of these species, contributing 7.9% of the diet, were not eaten in 1988–1989. When only the 25 species are considered, Schoener’s overlap between the two time periods was 63.1%. Eight of the 25 selected diet species were eaten in 1988 but not in 2000–2001, whereas two were eaten only in 2000–2001 (Table II). The frequency of feeding by mangabeys on the 25 diet species differed significantly between 1988 and 2000–2001 ($Z = -2.043$; $P = 0.041$; Table II).

Despite a three-fold increase in group size, mangabeys displayed narrower dietary preferences in 2000–2001 than in 1988 with selection indices ≥ 1 for only eight species in 2000–2001 but for 13 species in 1988 (Table III). Five of the species with indices ≥ 1 in 2000–2001 had similarly high indices in 1988. The three exceptions included *Sterculia appendiculata* and *Blighia unijugata*, two species that never fruited during the first study, and *Sorindea madagascariensis*. Seven of the ten most selected species in 1988 were not eaten by the group in 2000–2001: *Tamarindus indica*, *Ficus bubu*, *Lannea schweinfurthii*, *Cynometra lukei*, *Aporrhiza paniculata*, *Ficus natalensis*, and

TABLE II. Comparison Between 1988 and 2000–2001 in the Abundance of Reproductively Sized Individuals of 25 Species in 16.25 ha of Mchelelo West Forest, in Mean DBH of Phenology Trees, and in the Number of Feeding Events on Those 25 Species

Species	1988 abundance	2000–2001 abundance	1988 mean DBH \pm SE	2000–2001 mean DBH \pm SE	1988 events in diet	2000–2001 events in diet
<i>Alangium salviifolium</i>	545	776	42.9 \pm 5.7	37.0 \pm 9.3	50	10
<i>Lannea schweinfurthii</i>	9	9			71	0
<i>Sorindea madagascariensis</i>	110	173	55.2 \pm 4.9	37.1 \pm 7.4	47	100
<i>Rawolfia mombasiana</i>	845	87			21	5
<i>Saba comorensis</i>	14	27			48	5
<i>Cordia goetzei</i>	75	186			11	33
<i>Cynometra lukei</i>	7	2			32	0
<i>Tamarindus indica</i>	8	10			107	0
<i>Diospyros mespiliformes</i>	125	137	89.2 \pm 7.0	84.6 \pm 12.0	124	220
<i>Oncoba spinosa</i>	105	119	29.2 \pm 3.6	18.9 \pm 3.3	230	45
<i>Garcinia livingstonei</i>	28	24			6	4
<i>Acacia robusta</i>	11	46	62.4 \pm 12.6	52.5 \pm 8.1	21	103
<i>Albizia glaberrima</i>	9	17			0	0
<i>Albizia gummifera</i>	27	106			5	6
<i>Ficus bubu</i>	1	1			15	0
<i>F. bussei</i>	1	1			0	0
<i>F. natalensis</i>	9	9			36	0
<i>F. sycomorus</i>	19	21	157.5 \pm 18.9	58.8 \pm 12.6	92	17
<i>Hyphaena compressa</i>	284	655			264	111
<i>Phoenix reclinata</i>	3146	3944			922	435
<i>Aporrhiza paniculata</i>	27	3			146	0
<i>Blighia unijugata</i>	14	10			0	7
<i>Mimusops fruticosa</i>	14	20	78.2 \pm 8.5	53.4 \pm 5.9	40	0
<i>Pachystela msolo</i>	5	5			1	0
<i>Sterculia appendiculata</i>	14	10			0	68
Other					274	241
Total abundance	5,452	6,398				

M. fruticosa. *M. fruticosa* never fruited in 2000–2001, whereas the six other species were all found at abundances less than ten individuals. The top ten species in each study ranked by number of feeding events have six species in common: *P. reclinata*, *H. compressa*, *D. mespiliformes*, *F. sycomorus*, *A. salviifolium*, and *Oncoba spinosa*.

DISCUSSION

Our study found changes in the availability of mangabey diet species and in mangabey feeding behavior between periods separated by 13 years. Some of the differences in feeding behavior reflect changes in food availability, underscoring the degree of behavioral and ecological plasticity in the Tana River mangabey.

Of the 25 diet species monitored in 1988 and 2001, 13 species had similar stem counts, whereas three species experienced declines and nine species showed dramatic increases. We attribute changes in diet species to a combination of factors including a decline in human disturbance, elephant loss, and changes in the river's hydrologic regime, each of which may affect the mortality and recruitment of individual species in different ways. Several species that increased in abundance are sun-loving, pioneer species (e.g., *H. compressa*, *A. gummifera*, *A. robusta*). These species are regenerating primarily along forest edges where human activities have decreased because the TRPNR was gazetted in the late 1970s. Although human disturbance of forest edge decreased with time at Mchelelo, the levels of illegal elephant killing simultaneously increased, resulting

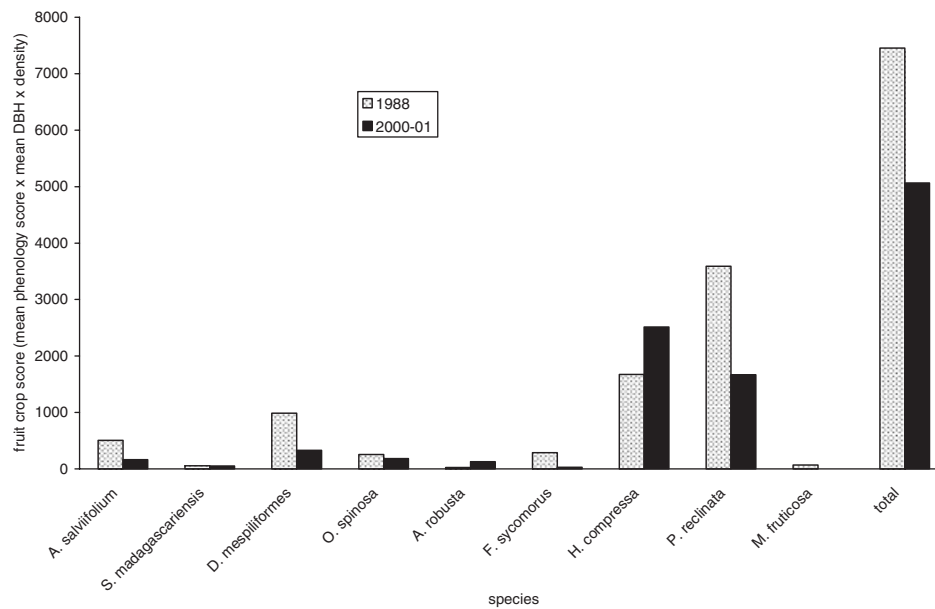


Fig. 2. Fruit crop scores for nine species individually and combined.

in the loss of the lower Tana River elephant population by 1989. Elephants elsewhere in Africa feed on *Acacia*, *Alangium*, and *Albizia* [Babaasa, 2000; Stokke, 1999]; these genera increased in our study, potentially benefiting from the absence of elephants. Chapman et al. [1997] similarly hypothesized that the lack of elephants in the Kanyawara area of Kibale NP, Uganda has resulted in an increase in densities of trees fed on by elephants. However, the growth and survival of some tree species are governed by recurring animal disturbances; this may explain why *Rauwolfia mombasiana*, a disturbance dependent tree [Höft, 1995], decreased nearly tenfold after elephants were removed. An additional factor potentially effecting forest change is the flooding regime. Hughes [1990] demonstrated the critical importance of river levels and flooding in the recruitment and mortality of Tana River forest trees. A number of dams constructed on the upper Tana River between 1968 and 1981 may have resulted in unfavorable regeneration conditions for some of the 25 diet species, most notably a lower suspended sediment load in the river [Kitheka et al., 2005], a decrease in flood pulse and number of inundation days per year as well as higher minimum flows [Maingi & Marsh, 2002].

Although each of the nine diet species in the Mchelelo West forest monitored for phenology increased in abundance between 1988 and 2001, estimates of overall fruit production were lower in 2001 than in 1988. We do not believe these differences are a result of observer bias; neither observer had consistently higher or lower scores than the other when compared by species or months.

Decreased fruit production may be a reflection of a younger demographic profile of Mchelelo trees in 2001 resulting, in part, from mortality of larger, mature trees during the 1997/1998 ENSO event [Wieczkowski, in preparation] and subsequent, high recruitment into the smaller size classes. DBH is known to be positively related to crown size and overall fruit production [Chapman et al., 1992; McDiarmid et al., 1977]; therefore, the smaller average DBH of Mchelelo trees in 2001 would be expected to have reduced fruit crops. Differences in fruit availability also may be influenced by changes in the river's hydrological regime. Because flowering is triggered by low river flows [Kinnaird, 1992b], the raising of minimum flow levels by upstream dams [Maingi & Marsh, 2002] may decrease flowering events or flower production and alter fruiting patterns. Differences in fruit availability between the two studies may also be because of regular interannual variation seen in the Tana River forests [Kinnaird, 1992b; Marsh, 1978b] and in other primate habitats [Chapman et al., 2005; Newstrom et al., 1994].

We found evidence that the change in consumption of 11 diet species might be explained by changes in stem abundance and/or fruit availability of those species. For example, the increase in *A. robusta* in the mangabey diet can be attributed to the dramatic increase in the stem abundance and fruit availability of this species. The absence of *A. paniculata* in the 2000–2001 mangabey diet may be tied to the near complete loss (from 27 individuals to three) of this species, whereas the absence of *M. fruticosa* can be attributed to the failure of that species to fruit in

TABLE III. Selection Indices of 23 Species in Each Study, With the Species Sorted According to the Selection Index

1988			2000–01		
Species	SI	Rank	Species	SI	Rank
<i>Tamarindus indica</i>	42	6	<i>S. appendiculata</i>	24	6
<i>Ficus bubu</i>	30	17	<i>A. robusta</i>	10.4	4
<i>Lannea schweinfurthii</i>	14	8	<i>D. mespiliformes</i>	7.4	2
<i>Cynometra lukei</i>	12	14	<i>F. sycomorus</i>	4	9
<i>Ficus sycomorus</i>	12	7	<i>S. madagascariensis</i>	2.6	5
<i>Aporrhiza paniculata</i>	11.4	4	<i>B. unijugata</i>	2.5	11
<i>Ficus natalensis</i>	7	13	<i>O. spinosa</i>	1.7	7
<i>Saba comorensis</i>	6.3	10	<i>S. comorensis</i>	1	13.5
<i>Mimusops fruticosa</i>	5.3	12	<i>C. goetzei</i>	0.8	8
<i>Oncoba spinosa</i>	4.7	3	<i>G. livingstonei</i>	0.8	15
<i>Acacia robusta</i>	4	15.5	<i>H. compressa</i>	0.8	3
<i>Diospyros mespiliformes</i>	2.1	5	<i>P. reclinata</i>	0.5	1
<i>Hyphaenae compressa</i>	2	2	<i>R. mombasiana</i>	0.3	13.5
<i>Sorindea madagascariensis</i>	0.9	11	<i>A. gummifera</i>	0.2	12
<i>Phoenix reclinata</i>	0.6	1	<i>A. salviifolium</i>	0.1	10
<i>Garcinia livingstonei</i>	0.4	19	<i>L. schweinfurthii</i>	0	0
<i>Albizia gummifera</i>	0.4	20	<i>C. lukei</i>	0	0
<i>Pachystela msolo</i>	0.4	21	<i>T. indica</i>	0	0
<i>Cordia goetzei</i>	0.3	18	<i>F. bubu</i>	0	0
<i>Alangium salviifolium</i>	0.2	9	<i>F. natalensis</i>	0	0
<i>Rauwolfia mombasiana</i>	0.1	15.5	<i>A. paniculata</i>	0	0
<i>Blighia unijugata</i>	0	0	<i>M. fruticosa</i>	0	0
<i>Sterculia appendiculata</i>	0	0	<i>P. msolo</i>	0	0

The rank based on number of feeding events is also given. SI, selection index; DBH, diameter at breast height.

2000–2001. Olupot [1998] attributed dietary differences in one group of *Lophocebus albigena johnstoni* over 20 years to temporal changes in composition and density of food trees as a result of increasing softwood plantations and regenerating forest [Olupot et al., 1994]. The change in consumption of 11 other diet species, however, are opposite from expectation based on the direction of changes in stem abundance and/or fruit availability. For example, *D. mespiliformes* fruit crop scores declined in 2001 (abundance stayed about constant), but mangabeys consumed more fruits and chose them more frequently than expected based on their availability at that time. And although abundance and fruit crop scores of *H. compressa* increased between studies, the species declined in importance in the diet. Chapman et al. [2002] found that some of the interannual variation observed in the red colobus diet could not be explained by differences in food availability. Nutritional analyses of the mangabey's foods may shed light on this question [Dasilva, 1994; Magliocca & Gautier-Hion, 2002].

Wieczkowski [2005] reported that the Mchelelo mangabey group increased in size between 1988 and 2001 from 17 to 50 individuals and concomitantly increased their home range from 19 to 47 ha; population density, however, stayed the same at 1.8 mangabeys/ha. The group expanded their home

range by traveling across regenerating scrub-woodland and using an adjacent forest area. The inclusion of this forest resulted in a comparable number of diet trees/mangabey between their smaller 1989 range (320 trees/mangabey) and their larger 2001 range (271 trees/mangabey). The increased home range may explain why the 2001 group's diet in Mchelelo West scored lower in all measures (smaller percentage of their diet from the 25 selected diet species, fewer overall species, fewer unique species, and lower preference scores for the 25 species) than the 1988 group's diet. Although the group spent 47% of their time outside Mchelelo West forest [Wieczkowski, unpublished data] where they encountered additional trees and additional species, dietary patterns in the full ranges remain substantially different between the two time periods.

Our data corroborate earlier studies demonstrating behavioral and ecological flexibility among Tana River mangabeys [Homewood, 1976; Kinnaird, 1990; Wieczkowski, 2003]. Dietary flexibility, as well as flexibility in grouping, intergroup interactions, and ranging [Homewood, 1976; Kinnaird, 1992c; Wieczkowski, 2005] allow the Tana River mangabey to persist in a habitat that is naturally dynamic and may ultimately allow them to persist in an environment strongly influenced by humans.

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