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Mortality trends in the African cherry (*Prunus africana*) and the implications for colobus monkeys (*Colobus guereza*) in Kakamega Forest, Kenya

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Abstract

Prunus africana (Hook.f.) Kalkm. is a secondary forest canopy tree species that has been declining over much of its geographical range in sub-Saharan Africa during recent decades due to unsustainable harvesting of its bark for the international medicinal plant trade. One of the locations where the species is experiencing rapid mortality is Isecheno study site in the Kakamega Forest, Kenya where this study was conducted. Between 1997 and 2003, 21% of the *P. africana* ($\geqslant$10 cm DBH) at Isecheno died and an additional 9% experienced $\geqslant$50% canopy dieback. However, scars from bark harvesting on *P. africana* were relatively small and scarred trees were not more likely to be dead or dying than unscarred trees, suggesting that bark exploitation is not causing *P. africana* mortality at Isecheno. Other possible causes that require further evaluation include disease, insect attack, nutrient deficiency, and/or climatic fluctuation. The poor regeneration of *P. africana* at Isecheno can likely be explained by the relative lack of recent disturbance coupled with the thick undergrowth layer at this site. *P. africana* mortality is of concern not only because the species is listed as Vulnerable by IUCN, but also because black and white colobus monkeys [*Colobus guereza* (Rüppell, 1835)] at Isecheno exploit it as their top food species and are particularly reliant on its leaves during times of 'preferred' Moraceae fruit scarcity. The anticipated continued decline of *P. africana* may have adverse effects on *C. guereza* feeding habits, intergroup relations, and population density at Isecheno. Conservation of *P. africana* offers a formidable challenge since the species appears to require disturbance for regeneration, yet at sites where disturbance is occurring, *P. africana* is often a target of bark harvesters engaging in unsustainable levels of exploitation.

Keywords: *Prunus africana*; *Colobus guereza*; Medicinal plant; Bark harvesting; Fallback resource

1. Introduction

Over the past several decades, African cherry [*Prunus africana* (Hook.f.) Kalkm.] populations have been declining in many forests due to unsustainable bark exploitation for the international medicinal plant trade (Cunningham and Mbenkum, 1993; Hall et al., 2000; Sunderland and Tako, 1999). Following the discovery in 1966 that an extract from *P. africana* bark effectively treats prostate gland hypertrophy and benign prostatic hyperplasia, pharmaceutical companies began hiring Africans to collect *P. africana* bark for export to Europe (Cunningham and Mbenkum, 1993; Ndibi and Kay, 1997). Since that time, the amount of *P. africana* bark stripped from African forests has increased exponentially, with a >17-fold increase during the period 1980–1999 alone (Anonymous, 2000). Unfortunately, much of this exploitation has been irresponsible with entire trees being girdled of their bark and left to die or, in other cases, felled to facilitate easier access to their bark (Cunningham and Mbenkum, 1993; Ndibi and Kay, 1997). This massive increase in the intensity of *P. africana* bark harvesting over a relatively short period prompted CITES to categorize the species as Appendix II (Cunningham et al., 1997) and IUCN to list it as

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Vulnerable (IUCN, 2002). Despite the protection afforded by these designations, however, *P. africana* remains Africa's most intensively exported medicinal plant species by volume (Cunningham et al., 2002).

Several studies and surveys have provided evidence of the adverse effects large-scale bark harvesting has on *P. africana* populations (Cunningham et al., 2002; Ndibi and Kay, 1997; Sunderland and Tako, 1999). For example, at Pico Basilé, Equatorial Guinea, Sunderland and Tako (1999) found that 68% of exploited *P. africana* were either dead or experiencing canopy dieback. Not all *P. africana* declines appear to be related to unsustainable bark harvesting practices, however. In a study of *P. africana* near the most southerly end of its geographic distribution along the Bloukrans River Gorge, South Africa, Geldenhuys (1981) found that 47% of the standing stems $\geqslant 10$ cm DBH were dead, but made no mention of bark harvesting. Instead, he attributed the mortality to increasing aridity in the Southern Cape region, which he believed no longer offered the climatic conditions necessary to maintain viable *P. africana* populations.

Though *P. africana* declines have been reported for forests in several African countries (Cunningham et al., 2002; Cunningham and Mbenkum, 1993; Sunderland and Tako, 1999), comparatively few efforts have been made to determine the wildlife that rely on *P. africana* as a food source. Anecdotal reports suggest that several endangered or near-threatened primate and bird species, including chimpanzees [*Pan troglodytes* (Blumenbach, 1799)] and gorillas [*Gorilla gorilla* (Matschie, 1903)] in Uganda and Preuss's guenon [*Cercopithecus preussi* (Matschie, 1898)], Bannerman's Turaco [*Tauraco bannermani* (Bates, 1923)], and the Cameroon Mountain Greenbul [*Andropadus montanus* (Reichenow, 1892)] in Cameroon, consume plant parts of *P. africana* (Cunningham and Mbenkum, 1993; Stanford and Nkurunungi, 2003). Observers in Kenya noted that mousebirds [*Colius striatus* (Gmelin, 1789)] and several species of greenbuls [*Andropadus gracilirostris* (Strickland, 1844), *A. latirostris* (Strickland, 1844), and *A. nigriceps* (Shelley, 1890)] eat *P. africana* fruits (Hall et al., 2000). In one of the few quantitative studies to date, *P. africana* accounted for up to 17% of the annual diet of red colobus monkeys [*Piliocolobus tephrosceles* (Elliot, 1907)] in the Kibale Forest, Uganda, and had the highest feeding time/stem density ratio of any tree species in the diet (Chapman and Chapman, 2002).

Another species of colobine monkey, the eastern black and white colobus or guereza [*Colobus guereza* (Rüppell, 1835)], relies even more heavily on *P. africana* in the Kakamega Forest, Kenya. During a study in 1997–1998, I found that despite its low stem density, *P. africana* was the top food species and contributed 20% and 19% to the annual diets of two guereza groups at Kakamega (Fashing, 2001a). In fact, during several months, *P. africana* accounted for as much as 30–50% of the diet. This intense reliance on *P. africana* by guerezas at Kakamega provides cause for concern in light of the *P. africana* declines that have been described elsewhere in Africa. Though they are considered to be among the most ecologically flexible of the arboreal African monkeys (Fashing, 2001a; Oates, 1977, 1994; Onderdonk and Chapman, 2000; Plumptre and Reynolds, 1994), a serious decline in their main food source might prove difficult for even guerezas to overcome.

Because *P. africana* is declining in many forests across its range and is such a vital component of the guereza diet at Kakamega, I studied changes in the *P. africana* population at Kakamega over a six-year period and evaluated possible links between these changes and anthropogenic disturbance. I found that a marked decrease in *P. africana* density occurred between 1997 and 2003, but that mortality over this period was unlikely to have been caused by bark exploitation. In this paper, I describe the pattern of this mortality, discuss its possible causes, provide evidence that *P. africana* is most important to guerezas as their fallback resource when other 'preferred' foods are not available, and discuss possible implications of *P. africana*'s decline for guerezas at Kakamega.

2. Methods

2.1. Study area

The Kakamega Forest (Fig. 1; 0°19′N; 34°52′E; Elev. 1580 m) is the easternmost remnant of the Guineo–Congolian rain forest system that once stretched virtually unbroken across much of equatorial and West Africa. Though the forest is listed as covering 240 km^2, indigenous forest accounts for only ~100 km^2 with the remainder being composed of plantations, tea fields, and grasslands (Brooks et al., 1999; Wass, 1995). The indigenous forest has been fragmented into at least two blocks, the largest of which is 86 km^2 (Brooks et al., 1999) and includes the site of central Isecheno where this research was conducted. The disturbance history of the forest includes past selective logging and several types of ongoing exploitation including charcoal burning, firewood and building material collection, and honey and traditional medicine harvesting (Fashing et al., 2004; Tsingalia, 1988). Levels of disturbance are heterogeneous across the forest with central Isecheno remaining less disturbed in recent decades than many other areas (Fashing et al., 2004). While some other sections of the forest were logged as recently as the early 1980s, Isecheno was last logged in the 1940s with *P. africana* included as one of the species targeted for logging (Tsingalia, 1988, N. Mitchell, personal communication).

Fig. 1. Distribution of *Prunus africana* across Africa (squares), location of Kakamega Forest (star and inset), and location of Isecheno study site (triangle). Modified (with permission) from Hall et al. (2000).

2.2. Study species

The African cherry is an evergreen canopy tree species typically reaching 25–30 m in height and occurs primarily in montane and middle-elevation forests (Beentje, 1994; Hall et al., 2000). It is distributed mostly along the eastern side of Africa from Ethiopia to South Africa, though there are populations in several West African countries and in the Comoros and Madagascar (Fig. 1; Hall et al., 2000). Seeds of *P. africana* germinate well under shady conditions but require light gaps to survive beyond the sapling stage (Kiama and Kiyiapi, 2001; Nzilani, 2002; Tsingalia, 1989). These traits have led most authors to refer to *P. africana* as a secondary forest species (Cunningham and Mbenkum, 1993; Geldenhuys, 1981; Sheldon et al., 1997; Stewart, 2003). In addition to its exploitation for the international medicinal plant trade, Africans have long used *P. africana* as a source of timber and traditional medicines (Cunningham and Cunningham, 1999; Hall et al., 2000; Stewart, 2003).

Guerezas are large arboreal monkeys that inhabit the forests of equatorial Africa from Ethiopia to Nigeria. They live in groups of 2–23 individuals and occupy relatively small home ranges within which they defend areas of intensive use against intrusions by other groups (Fashing, 1999; Oates, 1994). Guerezas at some locations are folivores (Bocian, 1997; Oates, 1977) while at others they can be more accurately regarded as folivore/frugivores (Fashing, 2001a; Poulsen et al., 2002). *C. guereza* is not regarded as a 'threatened' species (IUCN, 2002), though the subspecies at Kakamega, *C. g. matschiei* (Neumann, 1899), does have a relatively limited distribution in East Africa (Groves, 2001). The distribution and abundance of guerezas at Kakamega and nearby forest fragments have not been investigated outside of the research sites of Isecheno in the south (Fashing, 2002; Fashing and Cords, 2000) and Buyangu in the north (Gathua, 1995).

2.3. Prunus africana population monitoring

I first noted the locations of *P. africana* at central Isecheno while conducting a study of guereza behavioral ecology from November 1996–March 1998. Because guerezas spent much of their time in *P. africana* and individuals of this tree species were large and relatively uncommon, I became familiar with the locations of all of the *P. africana* $\geqslant 10$ cm DBH in the study area by ca. March 1997.

In February–March 2003, I returned to Isecheno and relocated the *P. africana* from my previous study occurring over an area of 0.47 km^2. For each individual, I measured GBH, which was then converted to DBH, and recorded the distance to the nearest trail from the base of the tree. I estimated canopy 'health' by recording the proportion of defoliated or dead limbs as 'few' (<10%), 'some' (10–49%), 'most' (50–99%), or 'all' (100%). Trees with a canopy health rating of few or some were regarded as 'living', those with a rating of 'most' as 'dying', and those with a rating of 'all' as 'dead'.

Along with two local assistants familiar with the medicinal uses of the forest's vegetation, I searched for evidence of bark stripping by humans in the form of basal scars (Hennon et al., 1990) on the trunk of each tree. The number of stripped areas per tree and the size of each stripped area were recorded. Volume of bark removed (Purohit et al., 2001) could not be assessed because, in most cases, stripping had occurred long enough ago that substantial bark regrowth had since occurred. I also recorded the height above the base of the tree at which each stripped area began. Stripped areas were classified as 'recent' or 'old'. Recent wounds were redder in color, exhibited few or no signs of bark regrowth, and were assumed to have occurred within the past year. I noted any peculiarities specific to particular trees, such as bark that appeared to have fallen off naturally or evidence of termite activity on the trunk (i.e., vertical red soil trails).

2.4. Prunus africana data analysis

Percent of trunk surface area stripped of bark (%*s*) was estimated roughly with the formula:

$$\%s = a/(h \times \pi) \times 100,$$

where a is the mean total area stripped per tree and h is the mean estimated trunk height of *P. africana* at Isecheno. The log model annual mortality rate (m) was calculated with the formula:

$$m = 100(\log_e n_0 - \log_e n_1)/t,$$

where n_0 is the number of individuals in 1997 and n_1 is the number surviving to 2003 after $t = 6$ years (Swaine and Lieberman, 1987). Population half-life ($t_{0.5}$) was calculated as

$$t_{0.5} = \log_e 0.5/0.01m.$$

Because most tree data collected in this study are not normally distributed, all statistical analyses presented are nonparametric. U values provided are from Mann–Whitney U tests, while r_s values are from Spearman rank correlations (Siegel and Castellan, 1988). All tests are two-tailed and significance was set at $p \leqslant 0.05$.

2.5. Colobus guereza feeding ecology

I studied the feeding ecology of two guereza groups, T and O, from March 1997–February 1998 (Fashing, 2001a). For each group, I collected dietary data via scan sampling at 15-min intervals from dawn-to-dusk on five consecutive days each month. If a monkey was feeding at the time of a scan, I recorded the plant species and food item upon which it was feeding. In several species with poor visibility into the canopy, including *P. africana*, leaves consumed could not be identified as young or mature with absolute certainty and were thus initially categorized as unidentified leaves. However, in the vast majority of instances (particularly involving *P. africana*), these unidentified leaves were believed to be mature based on circumstantial evidence (e.g., young leaf scarcity in the tree at the time feeding was observed, tendency of guerezas to apparently feed indiscriminately within clumps of mostly mature leaves, etc.).

Food availability for guerezas was evaluated via monthly monitoring of the phenological patterns of 13 tree species [*Albizia gummifera* (JF Gmel.) C.A. Sm., *Antiaris toxicaria* (Pers.) Lesch., *Celtis africana* Burm.f., *Celtis gomphophylla* Bak., *Croton megalocarpus* Hutch., *Ficus exasperata* Vahl, *Funtumia africana* (Benth.) Stapf, *Markhamia lutea* (Benth.) K.Schum., *Morus mesozygia* Stapf., *Prunus africana* (Hook.f.) Kalkm., *Teclea nobilis* Del., *Trilepisium madagascariense* DC., and *Zanthoxylum gillettii* (De Wild.) Waterm.] represented by 109 trees in T group's range and 101 trees in O group's range (Fashing, 2001a). Together these species ended up accounting for 83% and 74% of the annual diets in T and O groups, respectively. I conducted the phenological assessment of the trees in a group's range 1–4 days after I completed monthly dietary data collection for that group (Fashing, 2001a). I determined the relative abundance of leaf buds, young leaves, mature leaves, flowers, whole fruits, and seeds on each tree using Leitz 8 × 40 binoculars. I scored plant parts at intervals of 0.5 on a scale of 0.0–4.0 with 4.0 representing the score for a tree with the plant part at its greatest possible abundance, i.e., when the canopy was maximally laden with that part. I also assigned scores of very few and few to plant parts and gave them numeric values of 0.05 and 0.10 (Fashing, 2001a).

2.6. Colobus guereza data analysis

I computed a food item availability index (FAI) based on the monthly phenology scores and tree species biomass values for each study group's range using the following formula:

$$\text{FAI} = \text{average availability score} \times \text{basal area for species } i.$$

For nine tree species, *Antiaris toxicaria*, *Celtis africana*, *Croton megalocarpus*, *Ficus exasperata*, *Funtumia africana*, *Morus mesozygia*, *Prunus africana*, *Trilepisium madagascariense*, and *Zanthoxylum gillettii*, only individuals $\geqslant 125$ cm GBH (40 cm DBH) are included in the tree species biomass estimates for fruit availability because they appeared not to fruit until they were $\geqslant 125$ cm GBH (Fashing, 2001a). For the purposes of the data analyses conducted in this paper, all guereza feeding records on initially unclassified *P. africana* leaves were categorized as mature. As with the *P. africana* population monitoring data, statistical analyses on guereza feeding ecology were analyzed with nonparametric statistics, all tests were two-tailed, and statistical significance was set at $p \leqslant 0.05$ (Siegel and Castellan, 1988).

3. Results

3.1. Prunus africana population parameters

The locations of living, dead, and dying *P. africana* in the study area as of March 2003 are plotted on the map in Fig. 2. Between 1997 and 2003, 12 (21%) of the 58 *P. africana* at Isecheno died, resulting in a decline in population density from 123 to 98 ind/km^2. Annual mortality rate (m) was 3.9%, yielding a population half-life ($t_{0.5}$) of only 18 years. In addition to the 12 trees that died, 5 (9%) more exhibited >50% canopy dieback and were classified as dying in 2003 (Fig. 3). Only 28 (48%) individuals were regarded as having ‘few’ dead/defoliated limbs.

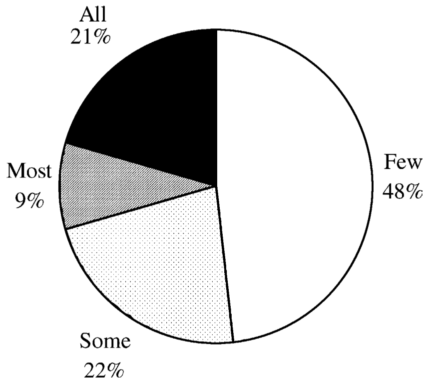

Fig. 3. Percent of *Prunus africana* at Isecheno ($n = 58$) classified as having ‘few’, ‘some’, ‘most’, or ‘all’ defoliated limbs.

A comparison of the stem size class distributions of living versus dead/dying *P. africana* does not reveal marked differences between these categories of individuals (Fig. 4). In fact, the mean DBH of living *P. africana* (mean $= 100.0 \pm 4.9$) is somewhat higher than that of dead/dying individuals (mean $= 87.9 \pm 6.3$), though this difference is not significant ($U = 258.5$, $n^1 = 41$, $n^2 = 15$, $p = 0.172$).

Evidence for spatial clumping among dead/dying individuals was mixed. The nearest conspecific individual was no more likely to be dead/dying for dead/dying trees than it was for living trees (G-test: $\chi^2 = 1.84$, df $= 1$,

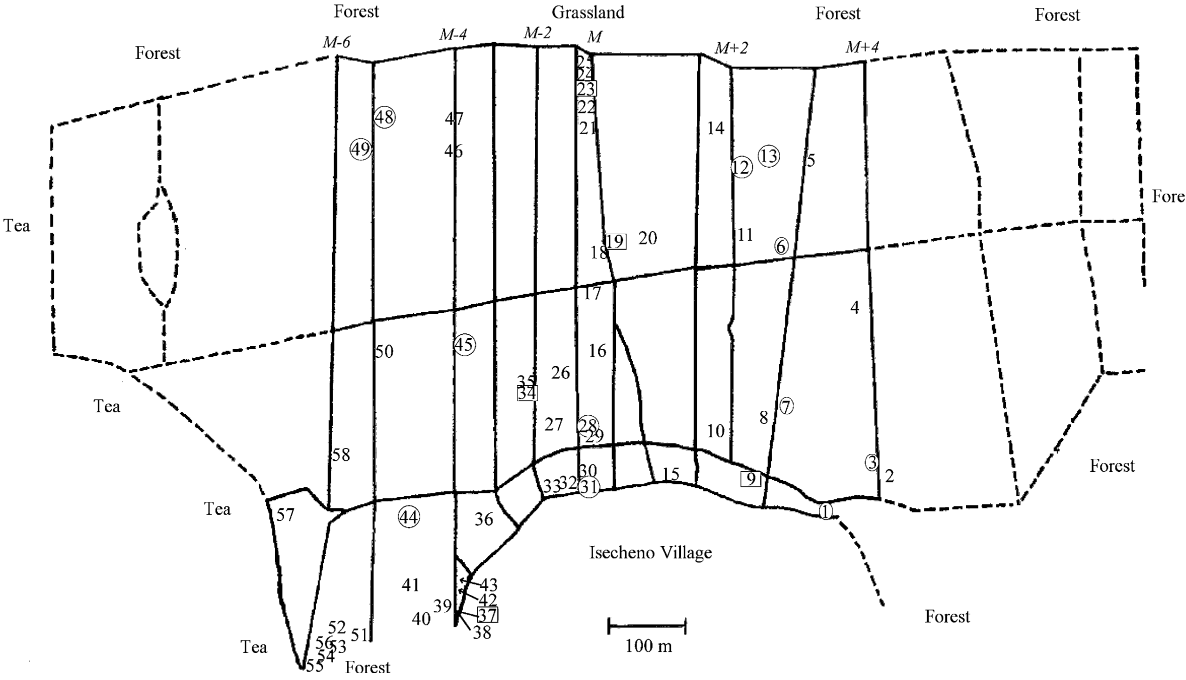

Fig. 2. Locations of the 58 *Prunus africana* monitored at Isecheno from 1997–2003. Squares signify that a tree is ‘dying’ ($\geqslant 50\%$ of canopy defoliated) and circles indicate that a tree is ‘dead’. All other trees are ‘living’ (<50% of canopy defoliated). Trail names are marked in italics (e.g., *M-6*). Trails and forest borders depicted with dashed lines fall outside the area where *P. africana* was monitored.

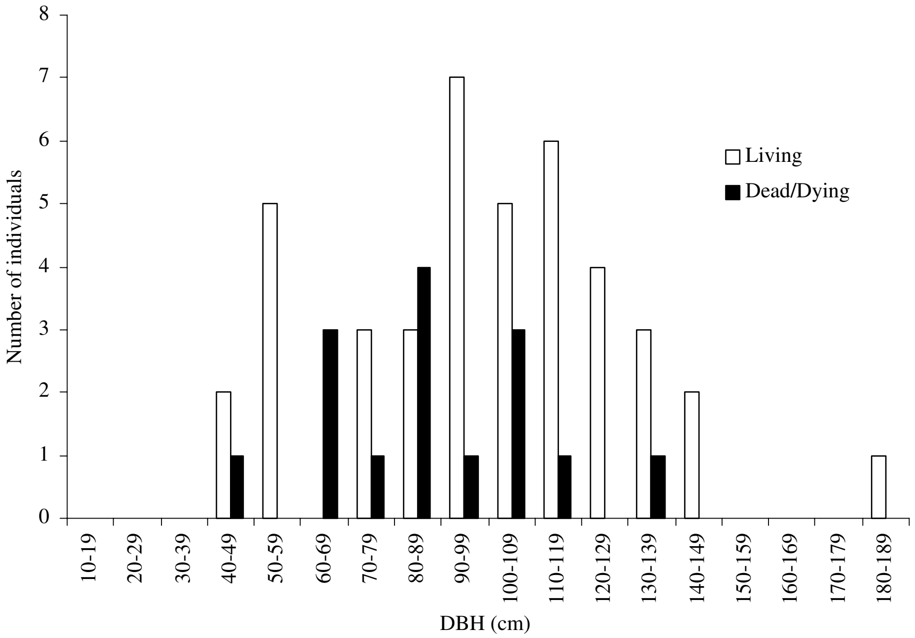

Fig. 4. Stem size class distributions of 41 living and 15 dead or dying *Prunus africana* ($\geqslant$10 cm DBH) at Isecheno. Note: Two additional dead trees could not be measured because they had fallen.

$p = 0.175$). However, individuals in the eastern quarter of the study area (E. of trail $M + 2$ on Fig. 2) were significantly more likely to be dead or dying (58%, $n = 12$) than those to the west (22%, $n = 46$; G-test: $\chi^2 = 5.70$, df = 1, $p = 0.017$). Evidence of termite activity was found on 57 of the 58 *P. africana* in the study area.

3.2. Patterns of Prunus africana bark exploitation by humans

A total of 91 basal scars were found on the 51 trees for which scarring could be confidently assessed. Scars typically took the shape of geometric patterns (rectangles, squares, etc.) almost certainly resulting from human cutting with *pangas*. No animal bite marks were found around scars. Most scars began 0–100 cm (mean = 55.7 ± 4.4 cm) above the base of the tree, often along buttressed roots. Only 10% of scars were classified as 'recent'. Trees averaged 1.8 ± 0.3 scars per individual for a total average area stripped per tree of 1803.2 ± 316.4 cm^2. Based on a rough estimate of the total bark available on the bole of each tree assuming a cylindrical shape and a mean height of 30 m, this stripping resulted in the removal of 0.20% of the total bark per tree.

Living trees (mean = 2.0 ± 0.3) had more scars per tree than dead/dying trees (mean = 1.0 ± 0.4), though this difference was not significant ($U = 126.0$, $n^1 = 41$, $n^2 = 10$, $p = 0.128$). Total area scarred per tree was also higher for living (mean = 1997 ± 372) than for dead/dying trees (mean = 1009 ± 473), though this difference was also not significant ($U = 147.0$, $n^1 = 41$, $n^2 = 10$, $p = 0.165$).

Neither number of scars ($r_s = 0.076$, $p = 0.596$) nor total area scarred ($r_s = -0.052$, $p = 0.712$) were correlated with DBH. In fact, both the smallest (44 cm DBH) and largest individuals (189 cm DBH) in the population showed evidence of scarring.

Both number of scars ($r_s = -0.459$, $p = 0.001$) and total area scarred ($r_s = -0.408$, $p = 0.004$) exhibited significant negative correlations with the distance of trees from the nearest trail. Living and dead/dying trees did not, however, differ significantly in their distance from the nearest trail ($U = 317.5$, $n^1 = 41$, $n^2 = 17$, $p = 0.395$).

3.3. Guereza reliance on Prunus africana

From March 1997 to February 1998, a total of 2211 and 2043 feeding records were collected for T and O groups, respectively. The diets of both groups consisted mostly of leaves (T: $n = 1064$ (48%); O: $n = 1173$ (57%)), though fruit (T: $n = 973$ (44%); O: $n = 676$ (33%)) made a substantial contribution to their diets as well. *P. africana* was by far the top food species in the annual diets of both groups, accounting for 439 (20%) of the feeding records in T group and 379 (19%) of the records in O group (Table 1). Nearly all of this *P. africana* consumption was on leaves, most of which were believed to be mature. In both groups, the species second most often exploited for its leaves, *Celtis africana* (T: $n = 208$; O: $n = 135$), accounted for less than half as

Table 1
Percent of time spent feeding on specific food items for the top six species in the diets of *Colobus guereza* groups T ($n = 2211$ feeding records) and O ($n = 2043$ feeding records) from March 1997 to February 1998

Rank	Species	Family	Young leaves[a]	Mature leaves	Unclass leaves	Fruit + seeds	Other	Total
T-Group								
1	*Prunus africana* (Hook.f.) Kalkman	Rosaceae	4.8	2.4	12.4[b]		0.3	19.9
2	*Ficus exasperata* Vahl	Moraceae	1.3		0.5	10.0	0.2	12.1
3	*Teclea nobilis* Del.	Rutaceae	1.9		0.1	7.7	2.0	11.7
4	*Trilepisium madagascariense* DC.	Moraceae			0.2	8.7	1.6	10.5
5	*Antiaris toxicaria* (Pers.) Lesch.	Moraceae				9.8	0.1	9.8
6	*Celtis africana* Burm. f.	Ulmaceae	9.1	0.1	0.3		0.2	9.7
	Top six sp. combined		17.1	2.4	13.5	36.3	4.4	73.7
O-Group								
1	*Prunus africana* (Hook.f.) Kalkman	Rosaceae	1.0	2.5	15.0[b]		0.1	18.6
2	*Trilepisium madagascariense* DC.	Moraceae			0.2	11.1	1.5	12.8
3	*Ficus exasperata* Vahl	Moraceae	1.2		0.5	6.0	0.4	8.1
4	*Celtis africana* Burm. f.	Ulmaceae	5.4		1.2		0.1	6.7
5	*Antiaris toxicaria* (Pers.) Lesch.	Moraceae				6.3	0.2	6.5
6	*Teclea nobilis* Del.	Rutaceae	0.8		0.1	4.3	0.6	5.8
	Top six sp. combined		8.5	2.5	17.0	27.7	2.7	58.4

[a] Includes young leaves and leaf buds combined.

[b] Believed to be mature leaves.

many leaf feeding records as *P. africana*. Fruits were consumed mostly from species belonging to the Moraceae family, particularly *Ficus exasperata*, *Trilepisium madagascariense*, and *Antiaris toxicaria*.

There was considerable intermonthly variation in consumption of the major food species with most ranking among the top five species during fewer than six months of the year. Only *P. africana* (T: 11 mo.; O: 10 mo.), and to a lesser extent, *C. africana* (T: 9 mo.; O: 7 mo.), ranked consistently among the five most exploited species per month. However, even *P. africana*'s relative contribution to the diet varied considerably among months (T: 0–42% of feeding records; O: 2–50% of feeding records).

A detailed examination of the relationship between the consumption of *P. africana* leaves and Moraceae fruit, and their respective availabilities, suggests that guerezas "prefer" Moraceae fruit and rely on *P. africana* leaves as their fallback resource when Moraceae fruit is scarce. Significant positive correlations existed between the consumption of Moraceae fruit and its availability for both study groups (T: $r_s = 0.755$, $p = 0.012$; O: $r_s = 0.874$, $p = 0.004$). These correlations were much stronger than those between *P. africana* young leaf consumption and availability (T: $r_s = 0.583$, $p = 0.053$; O: $r_s = 0.354$, $p = 0.241$) or between *P. africana* mature leaf consumption and availability (T: $r_s = 0.140$, $p = 0.642$; O: $r_s = -0.014$, $p = 0.963$). Furthermore, T and O groups increased their *P. africana* leaf consumption by 227% and 320%, respectively, during months of low Moraceae fruit availability (<70,000 FAI units/ha). Consumption of *P. africana* mature leaves in particular tends to be highest during those periods of the year when "preferred" Moraceae fruits are scarce (Fig. 5; T: $r_s = -0.729$, $p = 0.016$; O: $r_s = -0.574$, $p = 0.057$). For example, during July 1997 when almost no Moraceae fruit was available, *P. africana* mature leaves accounted for nearly half of O group's feeding records. *P. africana* leaves therefore appear to be the fallback resource upon which guerezas at Isecheno rely most when preferred foods are scarce.

4. Discussion

4.1. *Prunus africana* population status at Isecheno

Several lines of evidence suggest that as in many other African forests (Cunningham and Mbenkum, 1993; Sunderland and Tako, 1999), *P. africana* is experiencing at least a localized decline in the Kakamega Forest. First, nearly 30% of the individuals that existed at Isecheno study site in 1997 were dead or dying when resurveyed six years later. Second, *P. africana*'s mortality rate of 3.9% at Isecheno is much higher than the typical tree mortality rates of 1–2% reported for most other tropical forests (Hart, 2001; Lieberman et al., 1985; Phillips et al., 1994; Swaine et al., 1987b). Third, the stem size class distribution for the species shows that there is currently no recruitment occurring into the smallest tree stem size classes (10–19, 20–29, 30–39 cm) at Isecheno. Furthermore, though my study did not examine stems <10 cm DBH, evidence from three separate short-term studies conducted over the past two

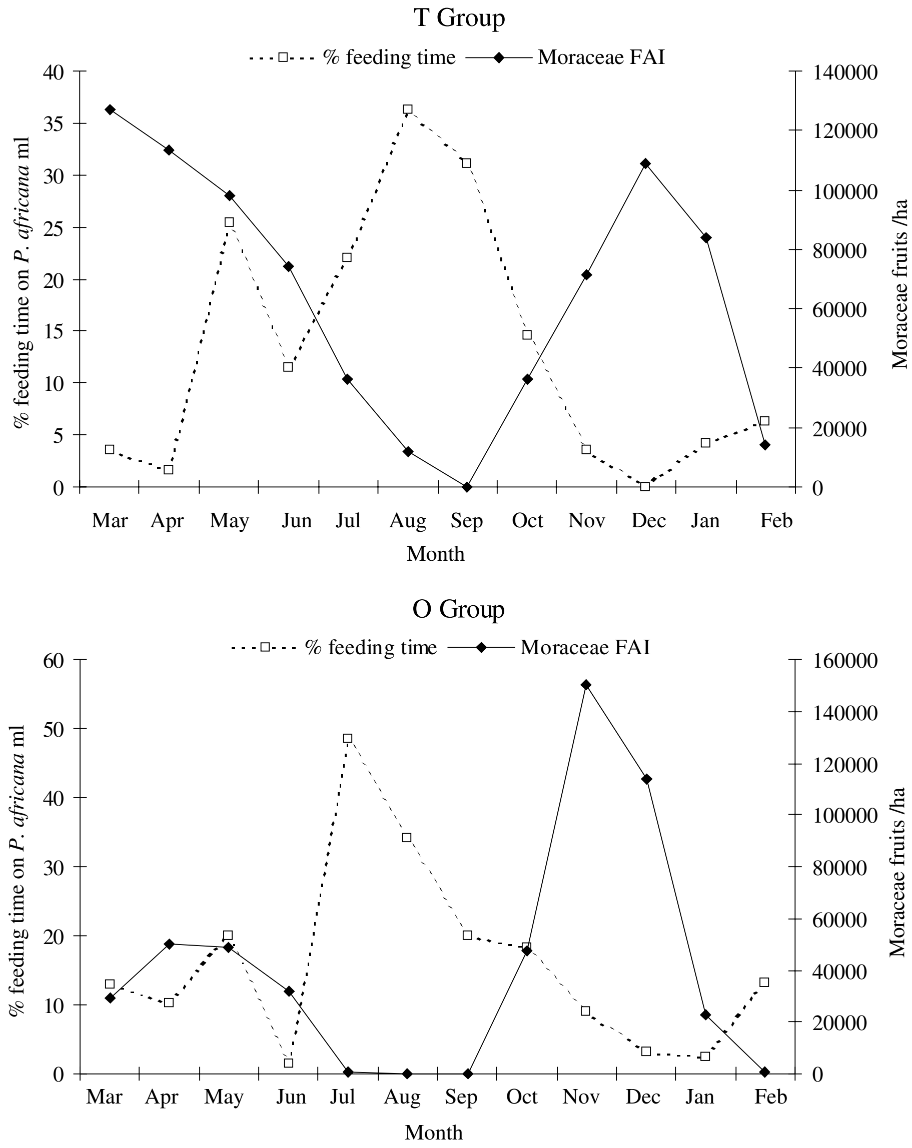

Fig. 5. Comparison of how *Prunus africana* mature leaf consumption varies with changes in Moraceae fruit availability for *Colobus guereza* groups T and O.

decades in Kakamega Forest suggests that *P. africana* seedling survival to the sapling stage has been extremely poor at several locations including Isecheno (Nzilani, 2001; Tsingalia, 1989, M. Kapitulnik, personal communication). The poor recruitment into the sapling and small tree classes coupled with the high mortality rate among trees >40 cm DBH suggests that the *P. africana* population at Isecheno will continue to decline for the foreseeable future.

4.2. Etiology of Prunus africana mortality at Isecheno

Based on reports from other African forests (Cunningham et al., 2002; Cunningham and Mbenkum, 1993; Sunderland and Tako, 1999), the agent originally expected to be most responsible for *P. africana* mortality at Isecheno was bark removal by humans. This hypothesis was not supported by the results of my study, however. Though most trees exhibited basal scarring, total area stripped per tree represented only a small fraction (ca. 0.20%) of the surface area of the trunk. Considering that some authors suggest that *P. africana* individuals can recover from removal of up to 50% of their bark (Cunningham and Mbenkum, 1993; Hall et al., 2000; Sheldon et al., 1997), the small amounts of bark stripped from trees at Isecheno are unlikely to be contributing to their mortality. Furthermore, dead/dying trees actually featured fewer scars and smaller total areas scarred than living trees. It therefore appears that bark harvesting is occurring at sustainable rates and is not responsible for the *P. africana* mortality at Isecheno. The low rate of exploitation at Isecheno also suggests that the large-scale bark harvesting for sale to pharmaceutical companies reported to be occurring in many African forests, including Kakamega (Cunningham et al., 2002), has not yet reached Isecheno.

Another hypothesis for the high rate of *P. africana* mortality at Isecheno is that the dead trees represent a cohort that perished through the *natural* process of senescence at roughly the same time. However, the facts that living trees had a larger mean DBH than dead/dying trees and that dead/dying trees exhibited extremely wide variation in DBH at Isecheno are inconsistent with this simultaneous senescence hypothesis. While it is true that the growth rates of conspecific individuals can vary considerably even within the same stand (Swaine et al., 1987a,b), it is unlikely that similarly-aged individuals would range in stem size class to the extent exhibited by the dead/dying *P. africana* at Isecheno (45–137 cm DBH).

Several other potential agents of *P. africana* mortality at Isecheno, including disease (Franklin et al., 1987; Waring, 1987), insect attack (Cunningham et al., 2002; Nair et al., 1996), nutrient deficiency (Gerrish et al., 1988; Hunter, 1993), and climatic fluctuation (Evenson, 1983; Lwanga, 2003), were not properly examined during this study and deserve future investigation. For example, the concentration of dead/dying trees in the eastern quarter of Isecheno raises concerns that disease may be playing a role in *P. africana* mortality at this site. Furthermore, the evidence of termite activity on 98% of the *P. africana* at Isecheno raises the possibility that insect damage could also be contributing to the decline.

As for the poor seedling survival described by others and the lack of recruitment into the smaller stem size classes reported in this study, natural forest succession processes may be to blame. Though their seeds germinate successfully in shaded conditions, the seedlings of *P. africana* appear to require large light gaps in the canopy to survive to the pole stage (Kiama and Kiyiapi, 2001; Nzilani, 2002; Tsingalia, 1989). At central Isecheno, in particular, anthropogenic disturbance has been limited in recent decades (Fashing et al., 2004) and probably has not been of sufficient severity to create the large light gaps required for the successful regeneration of *P. africana*. Furthermore, the dense undergrowth layer of Acanthaceae at Isecheno, believed to be a byproduct of the selective logging of the 1940s (Fashing and Gathua, in press), may play a role in inhibiting *P. africana* sapling survival at this site, much as it is believed to do in the forest on Mount Oku, Cameroon (Stewart, 2001).

4.3. Implications of *P. africana* mortality for guerezas at Isecheno

The high mortality and low recruitment rates of *P. africana* are likely to have negative repercussions for the animals that rely on the species as a food source at Isecheno. At present, the animal known to rely most heavily on *P. africana* at this site is the guereza. Not only is *P. africana* the guereza's top food item, its mature leaves appear to serve as their primary fallback resource when other more "preferred" foods (i.e., Moraceae fruit) are scarce. At the current rate of mortality, by 2021 guerezas living at Isecheno are predicted to have access to only one-half the currently available supply of their fallback resource. In a species that exhibits core area defense of its home range (Fashing, 1999; Oates, 1977) and defends food sources during encounters between groups (Fashing, 2001b), the anticipated decrease in *P. africana* density is expected to increase the rates and intensities of intergroup conflicts over time.

Though guerezas are often capable of adapting and even thriving in response to changes in their habitat (Plumptre and Reynolds, 1994; Struhsaker, 1997), recent evidence from fragments around the Kibale Forest, Uganda suggests that there is a point where habitat alterations begin to have adverse effects on guereza populations. Chapman et al. (2003) reported a 28% decline in guereza population density over just a five-year period in forest fragments subjected to intensive anthropogenic disturbance. Whether this decline was due to reductions in critical food sources is unclear, however, since changes in individual tree densities and guereza diets in these fragments were not reported.

The effects of staple food tree decline on population density have been studied in the vervet monkey [*Chlorocebus pygerythrus* (F. Cuvier, 1821)] population inhabiting the savanna woodland environment at Amboseli, Kenya (Lee and Hauser, 1998; Struhsaker, 1973, 1976). Like guerezas, vervets are regarded as ecologically-flexible primates, yet the Amboseli vervets experienced a marked population decline culminating in localized extinctions in association with a dramatic decline in their top food species, *Acacia xanthophloea*. While the rain forest ecosystem at Isecheno may buffer guerezas somewhat against experiencing a similarly drastic decline by providing a greater variety of potential alternative food sources, the vervet example provides evidence that even a pliable primate species may find it impossible to adapt to the decline of a staple food species.

Therefore, despite the guereza's reputation for resilience in the face of environmental degradation, the decline in *P. africana* density may prove to be difficult for guerezas at Isecheno to overcome. It will be important to continue monitoring both the population density (Fashing and Cords, 2000) and diet (Fashing, 2001a) of the guereza population over the coming years assuming *P. africana* continues its decline. Intriguingly, it may be the relative lack of recent anthropogenic disturbance in central Isecheno that accounts for the decline of the guereza's top food source at this site. If so, it suggests that maturation towards primary forest, while ostensibly laudable from an overall conservation perspective, may not be ideal for guerezas, a point that is consistent with Oates' (1977) contention that guerezas are best adapted to life in secondary forests.

4.4. Conservation strategies for Prunus africana

Conservation of *P. africana* offers a formidable challenge since the species appears to require disturbance for regeneration (Kiama and Kiyiapi, 2001; Tsingalia, 1989), yet at sites where disturbance is occurring, *P. africana* is often a target of bark harvesters engaging in unsustainable levels of exploitation (Cunningham and Mbenkum, 1993; Sunderland and Tako, 1999). Perhaps the best hope for in situ *P. africana* conservation lies in large montane forests with steep slopes like the Nyungwe Forest, Rwanda, where natural disturbances such as tree falls are common but commercialized bark exploitation has not been introduced (Plumptre et al., 2002, pers. observ). Based on the available case studies, it appears that once large-scale bark harvesting operations are initiated in a forest, the lure of a new source of income for impoverished local people quickly leads to unsustainable rates of exploitation (Cunningham et al., 2002; Cunningham and Mbenkum, 1993; Stewart, 2001; Sunderland and Tako, 1999). To help meet the increasing international demand for *P. africana* bark extract, generate income for local people, and reduce the pressure on natural forest populations of *P. africana,* it is critical that large *P. africana* plantations are soon established and rural farmers are encouraged to grow the species on their properties (Cunningham et al., 2002; Cunningham and Cunningham, 1999; Stewart, 2003).

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