
Effects of habitat disturbance and food supply on population densities of three primate species in the Kakamega Forest, Kenya

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Abstract

While habitat disturbance and food availability are major factors thought to determine the abundance of primates, evidence for their importance is uneven. We assessed the effects of these factors on three monkey species, guerezas (*Colobus guereza*), blue monkeys (*Cercopithecus mitis*) and redtails (*Cercopithecus ascanius*), in four areas of the Kakamega Forest, Kenya. Group densities of guerezas and blue monkeys were higher in areas where disturbance levels were also higher. Food availability measured as basal area density of food trees did not correlate significantly with the group densities of any of the three monkeys. The diversity of food trees, another potential measure of food abundance did, however, correlate with group densities of guerezas and blue monkeys suggesting that food availability may positively influence monkey density, and may sometimes increase with disturbance. Group densities of redtails did not correlate with any habitat variable examined, suggesting that factors other than those we considered may have influenced the abundance of this species particularly.

Key words: abundance, conservation, disturbance, food supply, population density, primates

Résumé

Alors qu'on pense que ce sont les perturbations de l'habitat et la disponibilité de la nourriture qui déterminent l'abondance des primates, les preuves de cette importance sont mitigées. Nous avons étudié les effets de ces facteurs sur trois espèces de singes, le colobe guereza (*Colobus guereza*), le cercopithèque à diadème (*Cercopithecus mitis*) et le

cercopithèque ascagne (*Cercopithecus ascanius*), dans quatre zones de la forêt de Kakamega, au Kenya. La densité des troupes de guerezas et de cercopithèques à diadème était plus forte dans les zones où le niveau de perturbation était plus élevé. La disponibilité de la nourriture, mesurée par la densité d'arbres alimentaires par unité de surface, ne montrait pas de corrélation positive avec la densité des troupes d'aucune des trois espèces de singes. La diversité des arbres alimentaires, autre mesure potentielle de l'abondance de nourriture, montrait une corrélation avec les troupes de guerezas et de *mitis*, suggérant que la disponibilité de la nourriture pourrait influencer positivement la densité des singes, et qu'elle peut parfois augmenter avec les perturbations. La densité des troupes d'*ascanius* ne montrait de corrélation avec aucune des variables de l'habitat étudiée, ce qui suggère que d'autres facteurs que ceux que nous avons étudiés pourraient avoir influencé particulièrement l'abondance de cette espèce.

Introduction

Tropical forests are often subject to both legal and illegal human activities resulting in forest loss and fragmentation, as well as changes in vegetation structure and composition that may affect forest dwelling animals (Cowlshaw & Dunbar, 2000). The conservation of organisms living in tropical forests depends on their ability to withstand anthropogenic habitat disturbance (Onderdonk & Chapman, 2000). Most primate populations today face ongoing habitat disturbance (Mittermeier *et al.*, 2006) and its effects are likely to increase as human populations grow. The exact effects of disturbance vary, however, depending on the primate and habitat (Skorupa, 1988; Plumptre &

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Johns, 2001). For example, chimpanzee (*Pan troglodytes*) densities increased with disturbance in Lope, Gabon but decreased in Kalinzu, Uganda (Plumptre & Johns, 2001). Effects of disturbance also vary according to its intensity and nature (Fimbel, 1994), which may explain inter-population differences in its consequences (Plumptre & Johns, 2001). While disturbance may negatively influence primates through habitat change and reduced food availability (Fimbel, Grajal & Robinson, 2001), disturbance may also increase food availability by promoting highly productive pioneer plants (Johns, 1988, 1991).

Food supply in itself is believed to be an important determinant of primate abundance that limits many populations (Cowlshaw & Dunbar, 2000; Marshall, 2004; Rode *et al.*, 2006; Rovero & Struhsaker, 2007). For example, although monkey populations in Gabon were affected by factors such as vegetation structure, competition, disease and predation, food availability was the most important (Brugiere *et al.*, 2002). In western Uganda, Chapman *et al.* (2002a, 2004) reported that population biomass of guerezas increased with the protein-to-fibre ratio of mature leaves. The authors suggested that this ratio indexes availability of important high-quality foods. In eastern Kenya, red colobus (*Procolobus rufomitratu*s) group densities in riverine forest patches correlated with basal area and density of food trees (Mbora & Meikle, 2004), while *Procolobus gordonorum* abundance in Tanzania's Udzungwa mountains correlated with species richness of food plants and basal areas of large trees (DBH ≥ 20 cm) thought to represent potential food sources (Rovero & Struhsaker, 2007). Rode *et al.* (2006) implicated one particular critical nutrient; they found that copper intake per calorie consumed correlated with population densities of redbills (*Cercopithecus ascanius*) across five habitats in Kibale National Park, Uganda.

Not all studies, however, have demonstrated a positive correlation between food availability and primate population densities. Skorupa (1988), for example, found that food availability (measured as basal area density of food trees) in Kibale correlated with the population densities of only one of four primate species. Similarly, there was no correlation between basal area of food trees and group density of redbill monkeys near Mpanga Forest Reserve, Uganda (Baranga, 2004a). Butynski (1990) studied two subpopulations of blue monkeys in Kibale and found higher food availability where monkey density was lower, contrary to expectations if food were the primary factor limiting population size. Similarly, Teelen (2007) found that different group densities of blue monkeys and guerezas

in five parts of Kibale's Ngogo field site could not be explained by differentially abundant food trees.

Overall, the effects of food supply and habitat disturbance on primate densities appear complex and are not yet fully understood. Our study examined how food availability and anthropogenic habitat disturbance affect population densities of three monkeys, guerezas (*Colobus guereza matschiei*) and blue and redbill guenons (*Cercopithecus mitis stuhlmanni* and *C. ascanius schmidti*), across four areas in the Kakamega Forest, Kenya.

Materials and methods

Study area

The Kakamega Forest is part of the Guineo-Congolian rainforest that once stretched across equatorial Africa (Tsingalia, 1990; Fashing, 2001). Although its gazetted area is c. 240 km², less than half now contains indigenous forest (Lung, 2004; Mitchell, Lung & Schaab, 2006); in some areas, vegetation is regenerating (Lung & Schaab, 2004). Elevation is 1400–1700 m (Fashing & Cords, 2000) and annual rainfall averaged 2007 mm over a recent 19-year period (Bleher, Uster & Bergsdorf, 2006).

Although gazetted as a protected area in 1933, the forest faces ongoing habitat destruction and degradation by humans, both legally and illegally (Bleher *et al.*, 2006). Historically, commercial logging was the main cause of habitat destruction. A presidential decree in the mid-1990s banned commercial exploitation of indigenous trees, after more than half the original timber volume had been lost (Mitchell, 2004; Bleher *et al.*, 2006). Current activities contributing to habitat destruction include collection of firewood and building poles, charcoal burning, cattle grazing and tree debarking (Fashing *et al.*, 2004; Bleher *et al.*, 2006). For several reasons, including different management regimes, the southern part of the forest, where this study was conducted, has been exploited more intensively and habitat degradation is more evident (Bleher *et al.*, 2006). Our four study sites, separated by an average of 5.5 km, were characterized by different disturbance levels (Bleher *et al.*, 2006; Fig. 1).

Data collection

CM conducted all primate censuses from May 30th to August 22nd, 2005, using line-transect methods. Censuses were usually carried out in early morning (07:30–10:30)



Fig 1 Map of Kakamega Forest (actual forest vegetation) showing the four study sites (courtesy of Gertrud Schaab, BIOTA East Africa). From least to most disturbed, they were Yala, Isecheno-II, Ikuywa and Isecheno-I

and late afternoon (15:00–17:30) when monkeys are typically most active. Because of time constraints and to avoid further disturbance, we used pre-existing transects, one at each site, maintained by the BIOTA East Africa research team (Yala, Ikuywa and Isecheno II) and by MC (Isecheno I). These transects were 1.85–2 km long and were marked every 50 m. CM walked each transect 35 times at 1–1.5 km h⁻¹. Whenever a monkey group was seen, CM recorded time, species, location on transect, angle between transect and monkey (using a SUUNTO DP-65 compass), and animal-to-observer distance as determined by a LEICA Rangefinder 900 rangefinder with 1 meter accuracy.

Twenty vegetation plots (50 m × 10 m) straddled each transect, with combined area of 1 ha per site. All trees with girth at breast height ≥10 cm were identified to species. We measured canopy height and foliage density, but these variables did not differ across sites, and are not considered further.

We used the number of tree stumps per km as a measure of disturbance, as recommended by Bleher *et al.* (2006) who noted the relative importance of logging as an

indicator of human impact at Kakamega. MP counted all stumps within 10 m of each transect (both sides) in 2002 and 2004. For each stump, he estimated the time since cutting by examining the degree of decomposition and evidence of recent activity (wood chips, disturbed surrounding vegetation). In our analyses, we distinguished between trees freshly cut in 2004 (about a year before the 2005 monkey census), and those cut before 2002.

Data analysis

We calculated monkey group densities using the 'Whitesides method' as described by Fashing & Cords (2000). This method estimates transect width as the maximum reliable perpendicular transect-to-animal distance, incorporating species-specific mean group spread (Whitesides *et al.*, 1988). Transect-to-animal distance was calculated based on measurements of observer-animal distance and sighting angle (see above). Considering fundamental principles, Plumptre & Cox (2006) recently recommended using transect-to-animal distance (rather than observer-animal distance) to estimate transect width. They were noncommittal about incorporating group spread, but an earlier study at our site demonstrated that the 'Whitesides method' estimated group densities that most closely matched those derived from long-term monitoring of group ranging patterns (Fashing & Cords, 2000). In our analysis, we used group spread values as reported in Fashing & Cords (2000). We do not report relative abundance (groups per km), which some recommend as a solution to the difficulties of transect width estimation (Mitani, Struhsaker & Lwanga, 2000). For each monkey species, sites would be ordered identically when abundance was expressed as group density or as relative abundance.

We computed the precision of our estimates by expressing the 95% confidence interval of the mean number of groups sighted (per cumulative five-census block) as a percentage of that mean (NRC, 1981; Mitani *et al.*, 2000; Table 1). For each site, the precision estimates were plotted as a function of the cumulative number of censuses to evaluate the adequacy of our sample (NRC, 1981; Mitani *et al.*, 2000; Fig. 2).

We used food tree lists from long-term studies of the monkeys in this forest (Cords, 1984, 1987; Fashing, 1999, 2001) to identify important trees in each species' diet. Basal areas of food trees were calculated in two ways (a) by including as foods only those plant species that contributed ≥1% to the annual plant diet of each monkey species

Table 1 Between-site differences in total number of groups sighted, number of sightings per census walk (mean \pm SE), and calculated group densities (per km²). Sites are ordered from the least to the most disturbed (based on pre2002 disturbance levels). Groups sighted per census walk is included to give a feeling for variation in sighting frequency; however, group density was calculated using all sightings from 35 census walks per site

Site (census length in km)	Total number of groups sighted			Groups sighted per census walk			Group density (groups per km ²)		
	Guereza	Blue	Redtail	Guereza	Blue	Redtail	Guereza	Blue	Redtail
Yala (1.95)	26	61	47	0.74 \pm 0.13	1.74 \pm 0.11	1.34 \pm 0.11	3.69	4.32	4.41
Isecheno II (2.00)	44	77	27	1.26 \pm 0.17	2.20 \pm 0.19	0.77 \pm 0.12	6.18	5.68	3.32
Ikuywa (1.85)	24	75	52	0.68 \pm 0.12	2.14 \pm 0.19	1.48 \pm 0.16	4.35	6.42	5.64
Isecheno I (2.00)	67	90	39	1.91 \pm 0.18	2.57 \pm 0.17	1.11 \pm 0.16	9.12	6.46	4.03

(accounting cumulatively for *c.* 80% of the annual plant diet) and (b) by including all trees that contribute $\geq 10\%$ to the plant diet in any given month.

For blue and redbtail monkeys, whose diet also includes invertebrate prey (Cords, 1987), basal areas of food trees were additionally calculated by adding to the second calculation the tree species that the monkeys use as a source of invertebrates and that contributed $\geq 1\%$ to their total (annual) diet. No matter how trees were selected for inclusion, basal areas were calculated for all individuals with DBH ≥ 10 cm. We calculated the Simpson Diversity Index using all trees contributing at least 1% to the annual plant diet. We used nonparametric Spearman correlations to test for relationships between monkey group densities and habitat variables across the four sites. This method does not assume normally distributed data, and we were unable to confirm normally distributed data from only four sites.

Results

Group densities varied across sites for all three monkeys (Table 1). For guerezas and blue monkeys, they were the lowest in Yala and the highest in Isecheno-I. For redbtails, group densities were the lowest in Isecheno-II and the highest in Ikuywa. Precision estimates generally levelled off indicating that any additional censuses would not have improved our estimates (Fig. 2), with guerezas at Yala one possible exception.

Depending on which tree species were included, the rankings of sites by basal area densities of foods varied considerably (Table 2). For guereza and blue monkey foods, however, Yala consistently ranked the lowest. Yala and Isecheno-I consistently ranked the lowest and the second-lowest for redbtail foods. Isecheno II consistently

ranked the highest for guerezas. Relative diversity of food trees varied somewhat across sites and monkey species but was consistently the highest at Isecheno-I and the lowest at Yala (Table 3).

Group densities were not correlated with basal area densities of food trees for any monkey species, no matter which trees were included (Table 4). There was, however, a significant correlation across sites between diversity of food trees and group densities of guerezas and blue monkeys. Redtails did not show this pattern.

For blue monkeys, group densities correlated positively with disturbance, but only for pre2002 levels (Table 4). Pre2002 disturbance levels did not correlate with any measure of food tree basal area density, but they were correlated with food tree diversity for blue monkeys. Group densities of guerezas and redbtails did not correlate significantly with either 2004 or pre2002 disturbance levels, although for guerezas the correlation coefficients were high (0.80). Nevertheless, neither disturbance measure was correlated with guereza food abundance, measured either as basal area density or diversity.

Discussion

Primate abundance and food

Among the four areas of the Kakamega Forest we examined, there was a significant correlation between diversity of food trees and group densities of guerezas and blue monkeys. Somewhat surprisingly, however, there was no correlation between monkey group densities and basal area density of their respective food trees. This result may reflect the difficulty of assessing food abundance, the difficulty of assessing primate densities, or the small number of sites surveyed.

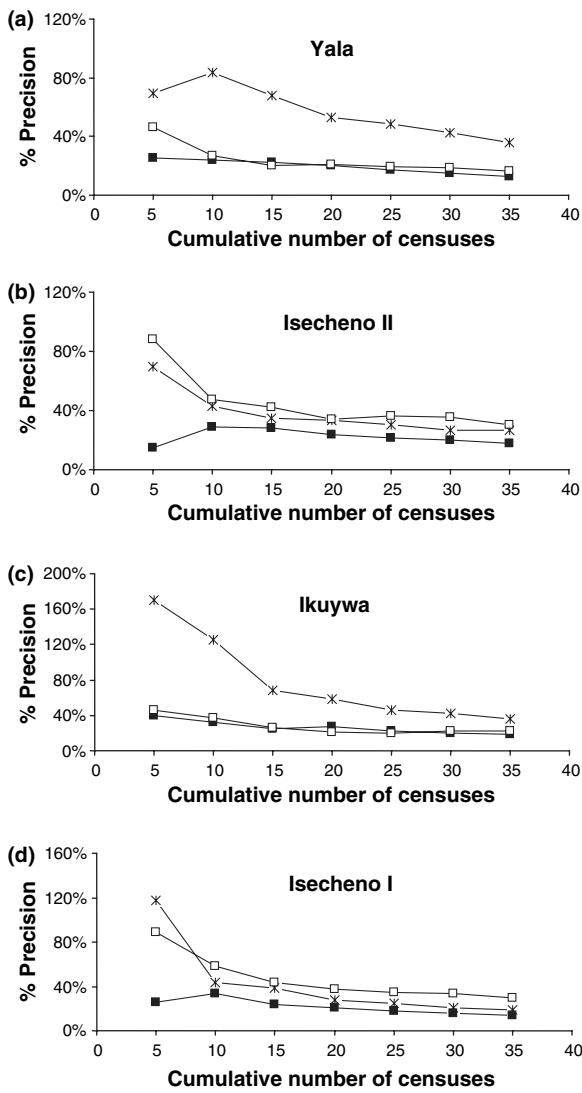


Fig 2 Precision of estimated mean number of groups per census at each site as a function of the cumulative number of censuses completed. Percentage of precision (vertical axis) = (95% CI/-mean number of social groups) × 100 (NRC, 1981). A lower percentage corresponds with greater precision in the estimated mean. Where lines flatten out, additional censuses do not improve precision. (Guerezas (X) Blue monkeys (■), Redtails (□))

Several factors may hinder accurate assessment of food availability. First, we cannot be certain that our food plant lists are complete. Although they derived from studies of ≥12 months, even such long-term studies may not identify all foods, and even all important foods, in a species' repertoire because of dietary variation among groups and over time (Chapman *et al.*, 2002b). Nonetheless, we note that

Table 2 Basal area densities of food trees ($m^2 ha^{-1}$) at each site for guerezas, blue and redtail monkeys using the two different tree samples: (i) all tree species contributing at least 1% to annual monkey diet; (ii) all tree species contributing at least 10% to the monkeys' plant diet in any given month. For blue and redtail monkeys basal area densities of food trees ($m^2 ha^{-1}$) were also calculated by adding to (ii) all tree species used as sources of invertebrates contributing at least 1% to the total annual diet. The number of species considered in each sample is given in parentheses. Sites are ordered from the least to the most disturbed (based on pre2002 disturbance levels)

Site	Guerezas				Blue monkeys				Redtail monkeys					
	≥1% of the annual plant diet (24)	≥10% of monthly plant diet (13)	≥1% of annual plant diet (26)	Rank	≥10% of monthly plant diet (14)	≥10% of monthly plant diet plus invertebrate sources ≥1% of total diet (17)	≥1% of annual plant diet (23)	Rank	≥10% of monthly plant diet plus invertebrate sources ≥1% of total diet (19)	Rank	Rank			
Yala	13.57	4	11.74	4	23.41	4	12.88	4	20.21	4	13.67	4	24.78	4
Isecheno II	41.47	1	38.89	1	40.35	2	30.84	1	40.04	1	34.08	2	41.48	1
Ikuywa	27.18	2	20.85	3	43.45	1	23.24	2	27.67	3	41.95	1	31.08	2
Isecheno I	23.98	3	22.25	2	34.84	3	23.09	3	30.46	2	29.64	3	29.19	3

Table 3 Simpson Diversity Indices for the food trees of each monkey species at each site, including species that contributed at least 1% to the annual diets ($n = 18$ for guerezas, $n = 26$ for blue monkeys, $n = 23$ for redtails). Sites are ordered from the least to the most disturbed (based on pre2002 disturbance levels)

Site	Guereza	Rank	Blue	Rank	Redtail	Rank
Yala	5.07	4	6.95	4	6.20	4
Isecheno II	7.53	2	9.63	3	8.25	3
Ikuywa	7.40	3	12.71	2	9.81	2
Isecheno I	10.77	1	13.05	1	13.23	1

others using similar datasets have documented positive correlations between food abundance and monkey density (Skorupa, 1988; Struhsaker, 1997; Chapman & Chapman, 1999; Worman & Chapman, 2006; Rovero & Struhsaker, 2007).

A second issue concerns the choice of food species to include in estimating food abundance. There is no consensus in the literature. For example, Wiczkowski (2004), studying Tana mangabeys (*Cercocebus galeritus*), used the top fifteen food species and two additional 'critical' species, one because it fruited when other important food species did not, another because it flowered asynchronously thus providing fruits year-round. Others have used the top five food species accounting for 75% (Chapman & Chapman, 1999; *Procolobus tephrosceles*) to 95% (Twinomugisha, Basuta & Chapman, 2003; *Cercopithecus mitis*) of the diet, or simply all species comprising 80% of feeding records (Skorupa, 1988; *C. mitis*, *P. tephrosceles*, *C. guereza*, *Lophocebus albigena*).

Our analyses also did not account for the fact that food plants, however defined, are not equally important in the diets of monkeys. In principle, one might weight the

species-specific basal areas according to frequency of use, or weight 'fallback foods' more heavily (Marshall & Leighton, 2006), but this procedure may be difficult because diets change over time and across groups in a single area (Chapman *et al.*, 2002b). Other studies documenting positive relationships between density and total food abundance (Skorupa, 1988; Struhsaker, 1997; Chapman & Chapman, 1999; Worman & Chapman, 2006; Rovero & Struhsaker, 2007) have not used such weightings either.

Another potential problem is that different tree species are reproductive at different growth stages. For example *Ficus exasperata* DBH must exceed 40 cm (Baranga, 2004b), while *Galliniera coffeoides*, *Xymalos monosopora* and *Lepidotrachia volkensii*, important food sources for golden monkeys (*Cercopithecus mitis kandti*), can fruit at DBH ≥ 5 cm (Twinomugisha *et al.*, 2003). Applying a fixed DBH cut-off across all food species fails to account for heterogeneous size-related variation in fruit production. Once again, however, other studies (Skorupa, 1988; Struhsaker, 1997; Chapman & Chapman, 1999; Worman & Chapman, 2006; Rovero & Struhsaker, 2007) have used the same criterion and nevertheless documented correlations between primates and their foods.

Isecheno-I's proximity to a forest station with horticultural trees may also have affected assessments of food availability. Monkeys sometimes ventured from the forest to feed, but the availability of these additional foods was not captured in basal area calculations because we measured only forest-interior trees. Similarly, Yala blue and redtail monkeys sometimes fed in a guava grove adjacent to the forest, but this grove was not included in vegetation surveys.

Although it is often used to assess food abundance, basal area density may not accurately capture important

Table 4 Results of the correlation analysis between group densities of each species and the three habitat variables considered in this study. Spearman correlation coefficients are shown. See Table 2 for full description of trees included in each basal area density calculation. Pre2002 disturbance levels include all trees cut before 2002. 2004 levels include all the trees cut before and in 2004

Species	Basal area densities of food trees ($\text{m}^2 \text{ha}^{-1}$)			Diversity	Disturbance	
	$\geq 1\%$ of annual plant diet	$\geq 10\%$ of monthly plant diet	$\geq 10\%$ of the plant diet in any given month and $\geq 1\%$ of total invertebrate diet		Pre 2002	2004
Guereza	0.40	0.80	N/A	1.00*	0.80	0.80
Blue monkey	0.40	0.20	0.40	1.00*	1.00*	0.40
Redtail	0.20	-0.40	-0.40	0.00	0.00	0.20

*Correlation is significant at the 0.01 level (two-tailed).

differences in abundance that are related to changes in food quality. Food quality can vary with canopy position (Schaefer & Schmidt, 2002) and across seasons. Worman & Chapman (2005) showed that lipid content of *Celtis durandii* fruits varied considerably over the year and consumption by three monkeys was sometimes very low even when fruits (with low lipid content at that time) were abundant. The abundance of a specific food measured by its basal area density could thus be unrelated to its value as a food source. In addition, the value of any particular food may depend on what else is available concurrently, so even abundant high-quality foods may be eaten infrequently at certain times.

As others have suggested, the availability of quality fallback foods may be especially but episodically important (Cant, 1980; Tutin *et al.*, 1997; Brugiére *et al.*, 2002; Marshall & Leighton, 2006). Furthermore, the identity of fallback foods for frugivores (like the guenons in this study) may vary over time and across taxa (Chapman *et al.*, 2005), making it difficult to study fallback food abundance in a comparative way without dietary data spanning many years. Such data are of course extremely rare.

Our estimate of primate abundance using group densities may have obscured a relationship between density and food abundance if group sizes varied among sites. Unfortunately, observation conditions and the widely spread blue and redtail monkey group members prevented us from estimating group sizes during censuses, so the extent to which results might have been affected remains uncertain. We note, however, that average redtail group sizes appear to vary little between Isecheno I and a site 11 km to the north (not included in our study, Gathua, 2000).

Our findings concur with several others (see Introduction) that showed no correlation between monkey and food plant densities, despite the fact that food availability and quality are often considered the most important limiting factors for primate populations (Cowlshaw & Dunbar, 2000; Brugiére *et al.*, 2002). Where correlations have been found, they are sometimes contradictory from study to study. For example, Worman & Chapman (2006) reported a positive correlation between population densities of blue monkeys and basal area of all food trees across two areas in the Kibale National Park. However, Butynski (1990), comparing two sites in another part of the forest, found that basal cover (total basal area of all trees per ha) was higher where the blue monkey population was lower. Seemingly conflicting results may result from different measures of food plant abundance. Wiczkowski's (2004) study of Tana mangabeys exemplifies

such effects, as she detected a correlation between monkey density and food abundance across forest patches only when she added to the top fifteen food species two additional plants that the monkeys were known to have eaten prior to her study. Conflicting results may, however, also result when factors influencing density, such as disease, have relatively local effects (Chapman & Chapman, 1999).

We found a strong correlation between food tree diversity and group densities of guerezas and blue monkeys, confirming previous reports. Thomas (1991) documented a significant correlation between food species diversity and population abundances of guenons in the Ituri Forest, Zaire. Lawes (1992) examined different subpopulations of samangos (*Cercopithecus mitis erythrarchus* and *C. m. labiatus*) across several forest types in Natal, South Africa and found that plant species richness and diversity predicted population densities. On a finer spatial scale, Rovero & Struhsaker (2007) also found that species richness affected red colobus densities. Although the underlying mechanism is unclear, it may be that higher diversity and species richness mean that more food is available throughout the year, especially during lean periods when fallback foods are the most important (Lawes, 1992; Cowlshaw & Dunbar, 2000).

It remains unclear; however, why redtail density did not correlate with food plant abundance. Some other factor may have influenced the density of this species, but not the other two.

Primate abundance and habitat disturbance

Delayed effects of disturbance on primate population densities are known from other sites. For example, in Kibale, more than 7 years was needed before the impact of moderate to heavy logging was reflected in monkey densities (Struhsaker, 1997; Chapman & Lambert, 2000). This fact may explain why we found no correlation between group densities and 2004 disturbance levels, while there was a correlation with pre-2002 disturbance levels, at least for blue monkeys. The lack of correlation for redtails may again reflect other factors affecting group densities (not captured in this study). For guerezas, the lack of correlation could result from the small sample size. Although the correlation coefficient was not significant, it was still high (0.80). Others have reported that guereza densities usually increase in disturbed habitats (Fashing, 2002, 2007).

Our analysis suggests that anthropogenic disturbance, at the levels we observed, does not negatively influence populations of guerezas and blue monkeys. On the contrary, their

group densities were higher in more disturbed sites. For blue monkeys, this effect may have been related to the greater diversity of food sources in more disturbed sites, but we did not find the same pattern for guerezas. Although redtail group densities were not correlated with disturbance, the fact that Ikuywa (most disturbed) had the highest redtail group density suggests that this species may be resilient to disturbance as well. In fact, others have shown that all three study species are resilient to some levels of disturbance or even show preferences for disturbed habitats. Specifically, Plumptre & Reynolds (1994) found that population densities of all three species in the Budongo Forest, Uganda were higher in logged areas. In the Ituri Forest, Zaire, all three showed strong preferences for secondary forest (Thomas, 1991).

Not all reports, however, support the view that disturbance has a positive, if any, effect on our study species or on primates generally. In Kibale, Chapman *et al.* (2000) found higher guereza densities in heavily logged areas, while redtail densities were higher in unlogged and lightly logged areas; for blue monkeys, the differences between logged sites and unlogged sites were insignificant. Populations of blue monkeys and redtails in heavily logged areas continued to decline decades after logging, although blue monkey densities were also declining in unlogged areas. In Natal, South Africa, Lawes (1992) found that samango group densities were consistently lower in areas with higher levels of disturbance. However, Muoria *et al.* (2003) found no significant relationship between group densities of five primates, including *Cercopithecus mitis albotorquatus*, and levels of forest destruction across several forest patches in the Tana delta, Kenya.

The effects of habitat disturbance on primates appear to vary because disturbance can influence the habitat in multiple ways and to different degrees (Fimbel, 1994; Chapman *et al.*, 2000; Onderdonk & Chapman, 2000). Also, how primates respond to disturbance may depend on site-specific factors like the possibility of moving to better quality habitat, or of re-colonization (Chapman *et al.*, 2000). In addition, population changes may occur gradually, leading to a temporary mismatch between disturbance and population consequences.

Conclusions

Because our study included a small number of sites, results should be interpreted with caution. The strong correlation between food tree diversity and group densities of guerezas

and blue monkeys suggests that food availability may be an important determinant of group densities for these species but measuring it in a meaningful way is not straightforward. The fact that redtail group densities did not correlate with any variables examined suggests that other factors influenced their abundance. The significant correlation between disturbance and group density of blue monkeys and the high correlation values for guerezas suggest that at least these monkeys are resilient to the levels of disturbance we observed. Redtails may show similar resilience, as their group density was the highest in the most disturbed site. How disturbance and food abundance relate to each other is not clear from our data, which suggest a correlation for blue monkey foods, but not for guereza foods.

Some authors argue that limited habitat disturbance and selective logging particularly may be compatible with conservation of at least some guenons as long as important fruit species are spared, refuge zones are established, forests are allowed to regenerate and anti-poaching measures are implemented (Matthews & Matthews, 2002). Our results concur with such a conclusion as it relates to blue and redtail guenons, and also with previous reports that guerezas thrive in somewhat disturbed forest (Lwanga, 2006; Fashing, 2007).

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