Status of Zanzibar Red Colobus and Sykes's Monkeys in Two Coastal Forests in 2005

Authors: Nowak, Katarzyna, and Lee, Phyllis C.

Source: Primate Conservation, 2013(27) : 65-73

Published By: Conservation International

URL: https://doi.org/10.1896/052.027.0107

Primate Conservation 2013 (27): 65–73

Status of Zanzibar Red Colobus and Sykes's Monkeys in Two Coastal Forests in 2005

Katarzyna Nowak[1,2] and Phyllis C. Lee[3]

[1]*Department of Zoology and Entomology, University of the Free State, Qwaqwa, Phuthaditjhaba, RSA*
[2]*Department of Anthropology, Durham University, Durham, UK*
[3]*Behaviour and Evolution Research Group, Psychology, University of Stirling, Scotland, UK*

Abstract: We censused two discrete subpopulations of the endangered Zanzibar red colobus (*Procolobus kirkii*) and sympatric Sykes's monkeys (*Cercopithecus mitis albogularis*) between February 2004 and September 2005 in two coastal forests in Zanzibar, including the northernmost (Kiwengwa-Pongwe Forest) and some of the southernmost (Uzi and Vundwe Islands) extents of *P. kirkii*'s range. Surveys totalled 365 hours and 307.8 km along >16 km of line transects; 472 sightings were made (Red colobus $n = 252$; Sykes's monkey $n = 220$). The southern forests (coral rag with adjacent mangrove) of Uzi and Vundwe Islands were found to support *P. kirkii* at a higher estimated density (29.6 groups/km²) relative to the northern coral rag forest (lacking mangrove) in Kiwengwa-Pongwe (7.5 groups/km²). However, for red colobus in coral rag, up to *c.*40% of these "groups" could be "sub-groups" based on our observations of consistent fission-fusion and small groups seen during the census (6.63 ± 0.4SE in Kiwengwa, 6.64 ± 0.33SE in Uzi) and behavioral follows in this habitat type. We therefore also include density estimates expressed as individuals/km² (49.72 individuals/km² in Kiwengwa, 196.32 individuals/km² in Uzi). On Uzi and Vundwe Islands, colobus densities were higher than those of Sykes's monkey (Sykes's monkey density = 18.9 groups/km²), while we found no difference between the density of these two taxa in Kiwengwa (Sykes's monkey density = 8.1 groups/km²) where encounters with humans were more frequent, vegetation was more disturbed, and the two species often associated. Although these populations represented a fraction of the historical total population of red colobus and Sykes's monkeys on Zanzibar, their estimated abundance was significant, and their marginal habitat and unprotected status were important in the general context of primate conservation in unprotected and fragmented landscapes.

Key Words: Coastal forest, mangrove, *Procolobus*, Sykes's monkey, Tanzania, island endemic

Introduction

Approximately 40% of *Procolobus* taxa are threatened with extinction (Struhsaker 2005). Of the five recognized species (Grubb *et al.* 2003; Grubb 2006), *P. pennantii*, *P. gordonorum*, and *P. kirkii* are Endangered (IUCN, 1990), and *P. rufomitratus* and *P. badius waldroni* are Critically Endangered (Oates *et al.* 2000; McGraw 2005; Roberts and Kitchener 2006). The most geographically isolated of these is the Zanzibar colobus *Procolobus kirkii* (Gray, 1868), known primarily from a population of about 1,500 in the largest protected area on Zanzibar, the Jozani-Chwaka Bay National Park (JCBNP) (Mturi 1991, 1993; Siex 2003). An island-wide presence/absence survey conducted between 1977 and 1981 found colobus groups living in 13 non-adjacent forest patches and estimated the species' Zanzibar-wide population at 1,700 individuals (Silkiluwasha 1981). Struhsaker and Siex (1994, 1996, 1998) made comparable estimates of fewer than 2,000 individuals more than a decade later. No population estimates are available for Sykes's monkey on Zanzibar.

Procolobus kirkii's resilience to habitat alteration is evident in its successful translocation to Masingini Forest Reserve, half of which is an exotic plantation (Struhsaker and Siex 1998), and its introduction to a novel but protected area (Ngezi Forest) on Pemba Island to which it is not native (Camperio-Ciani *et al.* 2001). While the species' colonizing ability may be high, competition with guenons, persecution by humans, and the high cost of translocation limit the options for such management strategies. The protection of populations where they naturally occur is preferable (Struhsaker and Siex 1998). The species' endangered and endemic status makes knowing their historical ranges and how many are left vital to their conservation and management of forest habitats. The highest density of red colobus (550 individuals/km²) was recorded in farms adjoining JCBNP (Struhsaker and Siex 1998; Siex and Struhsaker 1999), but no other systematic surveys outside this region had been conducted at the time of our study.

This census, carried out between 2004 and 2005, and followed up with visits, most recently in 2011, to confirm presence and persistence, aimed to describe subpopulations of *P. kirkii* to the north and south of the JCBNP: the northern Kiwengwa-Pongwe forest, and Uzi and Vundwe Islands in the south. Both areas supported indigenous coral rag and mangrove forest, and had a high potential value for sustaining red colobus populations on Zanzibar. Sympatric Sykes's monkeys (*Cercopithecus mitis albogularis*) were also censused to compare the habitat-use patterns of these two genera on Zanzibar and to understand responses to habitat degradation of related species and subspecies on the mainland (e.g., Udzungwa red colobus, *Procolobus gordonorum*; Struhsaker *et al.* [2004]).

Study Sites

The Kiwengwa-Pongwe forest (5°55′–6°04′S and 39°20′–39°23′E), now a Forest Reserve, and Uzi and Vundwe Islands (6°18′–6°24′S and 39°23′–39°26′E), which remain unprotected, are located on and adjacent, to Unguja, the largest island in the Zanzibar archipelago, which lies between 4°50′–6°30′S and 39°10′–39°90′E and makes up 63% of the total area (2,332 km²) of the archipelago. The topography of Unguja is predominantly flat with a highest point of 120 m above sea level. The eastern region has shallow, arid, coral-derived, high-calcium soils supporting low-canopy, semi-deciduous dry forest known as coral rag (Masoud *et al.* 2003).

Kiwengwa-Pongwe (hereafter "Kiwengwa") was a 33 km² forest composed of coral rag with a wide zone of transition to shrubland, scrub, and cultivation. Along the eastern edge, native forest had been cleared for plantations of *Casuarina equisetifolia*. Coral rag in Kiwengwa once supported canopy emergent trees such as *Terminalia boivinni*, *Mystroxylon aethiopicum, Mimusops fruticosa*, *Diospyros consolatae*, and *Ficus* spp. and an understory dominated by cycads (*Encephalartos hildebrandtii*), all of which were red colobus food plants (Nowak 2007; Nowak and Lee 2011a).

Uzi and Vundwe islands (hereafter "Uzi") are relatively isolated, connected to Unguja by a 3-km long, tidal isthmus of mangrove swamp in the north and surrounded by the Indian Ocean. Uzi has an area of 15.6 km², consisting of a matrix of cultivation, secondary coral rag forest, and scrub (Silkiluwasha 1981). There continues to be extensive clearing of coral rag forest on Uzi, and also, recently on Vundwe Island (Nowak *et al.* 2009). Remnant patches of high coral rag could still be found along Uzi Island's western side (known as "Mchangamle") at the time of this census (2004–2005); however, this forest was completely cleared between 2006 and 2009 (Mease 2009; Nowak *et al.* 2009). Mature mangrove stands still occur in the north and northwest, south and southeast. The northern Uzi mangroves border JCBNP, span *c.*592 ha, and were gazetted as part of a 1959 Forest Reserve Decree. They are interspersed with small coral rock island "stopovers", which once facilitated animal dispersal between Uzi and Jozani.

The southern area of Uzi was recommended for national park status by Struhsaker and Leland in 1980 as it provided the Zanzibar colobus with habitat types rare in Jozani. The southern extent of mangroves, dominated by *Rhizophora mucronata* (see Nowak 2008), adjoined, at the time of our study, coral rag forest with *Macphersonia gracilis*, *Eugenia capensis*, and *Polysphaeria parvifolia*; regenerating areas with pioneering species such as *Croton pseudopulchellus*; woody climbers such as *Monanthotaxis fornicata*; and beach vegetation , which included *Rhus natalensis*, *Vitex trifolia* and *Hibiscus tiliaceus* (see Nowak 2007).

Vundwe, a smaller (1.4 km²) and uninhabited island, lies 300 m from the southern tip of Uzi. Colobus have been reported by local people to cross between Uzi and Vundwe (*c.*300 m) at low tide. Vundwe Island had few mangroves and, at the time of this survey, still supported high coral rag forest with large baobab trees *Adansonia digitata* (see Nowak 2007). Vundwe is a popular commercial fishing site for fishermen from Unguja, Pemba, and mainland Tanzania.

No detailed studies on primates had been conducted at either of these two areas prior to Nowak (2007), although Silkiluwasha (1981) described Kiwengwa as 'low-density' and Uzi Island as 'high-density' with respect to colobus. Both regions were and continue to be subject to high levels of human disturbance, including firewood and pole extraction, lime making, cultivation, trapping of guineafowl (*Guttera pucherani* and *Numida meleagris*), and hunting, sometimes with dogs, of bushpig (*Potamochoerus larvatus*), and netting of duiker (*Cephalophus adersi* and *C. monticola*).

Methods

Transects

Seven line transects were established: four parallel transects with a total length of 10.55 km, ranging from 1,250 m to 3,850 m, and spaced 2 km apart in Kiwengwa; and two transects spaced approximately 2 km apart in western Uzi Island and one transect bisecting the length of Vundwe Island with a combined length of 5.65 km and ranging from 1,850 m to 2,050 m (Fig. 1). Using standard line-transect methods (Peres 1999), censuses were conducted monthly over 12 consecutive months from February 2004 to January 2005, with each transect randomly replicated 17 times. Censuses were repeated two additional times six months later along each transect from July 2005–September 2005, for a total of 19 repeated surveys and 200.45 km traversed in Kiwengwa and 107.35 km in Uzi. We opted for replicated surveys along the same lines over one-off surveys along many lines in order to monitor the same areas over time and reduce vegetation disturbance.

Before initiating surveys, distance estimates and recognition of red colobus age-sex classes (consistent with those

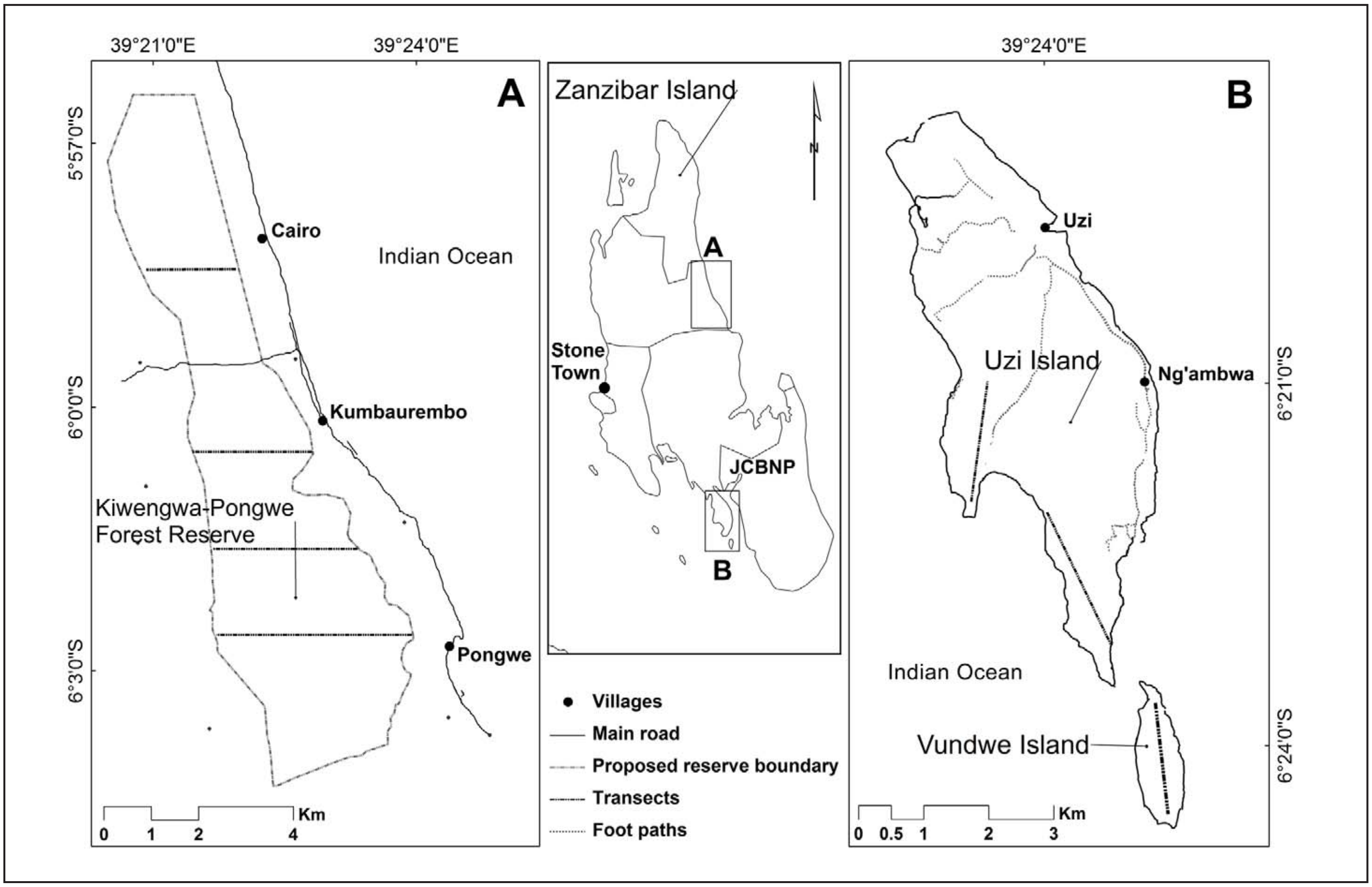

Figure 1. Study sites showing the locations of the line transects. **A.** Kiwengwa-Pongwe Forest Reserve, Zanzibar. **B.** Uzi and Vundwe islands, Zanzibar Archipelago, Tanzania.

used by Struhsaker [1975] and Siex [2003]) were practiced by observers (n = 4) until >80% inter-observer reliability was achieved. During encounters with colobus a cut-off of 10 minutes stationary (Marshall *et al.* 2005) was used before resuming the transect walk, and 5 minutes for the more rapidly moving Sykes's monkey. Records of humans, dogs, and signs of human disturbance along transects were also made and allotted approximately one minute for confirmation.

Statistical analyses were carried out in SPSS v. 16 (IBM Corporation).

Seasons and vegetation

Seasons were categorized into two wet and two dry periods on the basis of mean rainfall and temperature (Nowak 2007). Rainfall peaks occurred during the long rainy season, March–May (wet 2) and short rains occurred from October to December (wet 1). The extended dry season spanned June–September (dry 2) and the hottest dry period was between January and February (dry 1).

Vegetation was sampled every 50 m along transects in 5 × 50 m plots at the time of the census. All live woody stems ≥2.5 m in height were identified and measured. For multi-stemmed trees, the total number of live and cut stems was recorded, and the DBH of the five largest live and cut stems was measured (92% of cut stems were measured below breast height). A total of 84 plots was sampled in 2.1 ha (0.75 ha along Uzi and 1.35 ha along Kiwengwa transects). Plant species' density was calculated as the number of individuals per ha. Basal area (BA) was defined as the cross-sectional area of each tree at breast height using the formula: $BA = (\pi * DBH^2/4)$ (Larsen 1997). For multi-stemmed trees, basal area was calculated separately for each stem and then summed for a cumulative live stem BA. Plant phenology data were collected monthly for 13 months in Kiwengwa and 10 months in Uzi to index seasonality and availability of top colobus food plants (*n* = 16; Nowak, 2007) using an index from Siex (2003) that incorporates BA.

Population estimates

Population densities were estimated in *Distance* v. 5.0 with classic distance sampling using perpendicular distances (Buckland *et al.* 2001, 2010). Observations beyond 60 m were excluded. Data were checked for observer biases detecting large over small groups and no association was found between perpendicular distance and group size for red colobus (Kiwengwa, Spearman r_s = -0.089, *n* = 75, n.s.; Uzi, r_s = -0.025, *n* = 169, n.s.) nor for Sykes's monkeys (Kiwengwa, r_s = 0.144, *n* = 96, n.s.; Uzi, r_s = 0.007, *n* = 124, n.s.), suggesting that larger groups were neither detected more frequently nor at greater distances than smaller groups.

Habitat use

To compare habitat-use, chi-square tests were used on observed and expected numbers of sightings of both primate species in six habitat types, stratified according to plant species composition using correspondence analysis (Nowak 2007). Expected values of habitat use were calculated on the basis of habitat availability along transects, estimated in GIS using Google Earth imagery and ground-truthed. Five of the six habitat types (the sixth being *shamba* or cultivated area) represented a transition zone or gradient in species diversity and canopy height that progressed from low diversity shrubland to scrub to low, medium and high coral rag forest with distance from the forest edge.

Results

Encounters

We had 857 encounters with monkeys. "Vocalization-only" encounters with no follow-up sighting made up 45% of these encounters (n = 385). Of the remaining 55%, we detected colobus mainly by sight, while Sykes's monkeys were usually initially detected by vocalization and then visually detected (species by detection type, χ^2 = 6.076, df = 2, p = 0.048) similar to Fashing and Cords (2000). Since 41% of detections, especially of Sykes's monkeys, were made first by vocalization, detections based only on sound are potentially important indicators of density, especially in dense habitats, as for birds (Nelson and Fancy 1999; Lefebvre and Poulin 2003). The following analyses, however, are based only on encounters in which animals were seen, i.e. "sightings".

In total (over the 19 repeat surveys), we saw 361 colobus groups and recorded 1662 individuals (n_{Kiwengwa} = 130 groups, 503 individuals and n_{Uzi} = 231 groups, 1159 individuals) and 496 Sykes's monkey groups and 1,116 individuals (n_{Kiwengwa} = 275 groups, 471 individuals; n_{Uzi} = 221 groups, 645 individuals). More colobus groups were seen in Uzi than in Kiwengwa (Mann-Whitney U, Z = 7.43, df = 76, 57, p <0.001) and in Uzi, the minimum number of colobus groups seen on any census walk was between five and 14 while in Kiwengwa, the number of colobus groups seen on census ranged from one to eight. More colobus than Sykes's monkey groups were seen in Uzi (Wilcoxon Signed Ranks, Z = 3.26, n = 57, p <0.001), while no significant difference between the number of Sykes's monkey and colobus sightings was found in Kiwengwa (Wilcoxon Signed Ranks, Z = 0.97, n = 76, n.s.). Encounter rates (number of groups/km) of both colobus and Sykes's monkey were higher in Uzi than in Kiwengwa (colobus, t = -10.43, df = 131, p <0.001; Sykes's monkey, t = -4.95, df = 131, p <0.001) with a mean encounter rate of 0.38 (±0.15 SD) colobus groups/km and 0.57 (±0.70 SD) Sykes's monkey groups/km in Kiwengwa, and 1.63 colobus groups/km (±0.42 SD) and 1.16 (±0.69) Sykes's monkey groups/km in Uzi. The number of sightings did not vary with season (colobus: ANOVA, $F_{4, 23}$ = 0.69, n.s.; Sykes's monkey, $F_{4, 23}$ = 2.06, n.s.).

Density estimates

Sightings of both species at both sites were most frequent at 10–20 m from the observer, and the number of sightings dropped off at 50–60 m from the transect line. Following truncation at 60 m, there were no significant differences in sighting distances across vegetation types (Kiwengwa, F = 0.125, n.s.; Uzi, F = 0.315, n.s.).

Population density estimates are summarized in Table 1. Mean group sizes calculated in *Distance* are based on group sizes estimated on census. These are significantly smaller than those obtained from demographic monitoring of focal red colobus groups (Nowak and Lee 2011b) and represent sub-groups, incomplete counts of groups, or small groups, difficult to distinguish while surveying. However, given our observed fission-fusion of red colobus groups in coral rag forest, we also report density expressed as individuals/km² for colobus.

Mixed-species groups

On transects, Sykes's monkeys were more likely than colobus to occur alone. The proportion of all encounters that were with solitary individuals was 6.3% for colobus (n = 4 in Kiwengwa; n in Uzi = 12) and 11.8% for Sykes's monkey (n Kiwengwa= 11; n Uzi = 15). There were more sightings of mixed colobus-Sykes's monkey groups in Kiwengwa than in Uzi (χ^2 = 3.81 df = 1, p = 0.051). Of the 76 encounters with colobus in Kiwengwa, 18 (23.7%) were mixed colobus-Sykes's monkey groups. Of 176 colobus encounters in Uzi, 26 (14.8%) were mixed species. Overall and for each site separately, the frequency of mixed-species groups was independent of vegetation type (χ^2= 7.75, df = 5, n.s.; in Kiwengwa, χ^2 = 9.67, df = 5, n.s.; in Uzi, χ^2= 6.55, df = 4, n.s.).

Habitat preferences

An area of 21 000 m² was sampled in 84 plots along transects, and 16,460 trees were measured, representing 179 species from 55 families. The two sites were less similar in species composition than would be expected for sites separated

Table 1. Zanzibar red colobus and Sykes's monkey density and population abundance estimates ("Site N") derived from *Distance*.

Taxon	Site	N	Best-fit model	AIC	Groups/km²	S.E.	Individuals/km²	S.E.	Site N	S.E.
Red colobus	Kiwengwa	75	Half-normal	557.5	7.5	3.1	49.7	20.4	1149	471.8
	Uzi	174	Uniform	1294.5	29.6	2.5	196.3	17.7	1751	157.5
Sykes's monkey	Kiwengwa	96	Uniform	740.4	8.1	2.6			922	308.6
	Uzi	124	Hazard-rate	932.1	18.9	4.7			875	224.6

by less than <30 km with a score of 0.51 on the Sorensen similarity index. Roughly half (46%) of species in Uzi were not detected in Kiwengwa, and 50% of species in Kiwengwa were not detected in Uzi. Kiwengwa and Uzi both supported representatives of 13 site-specific families. The transect in Mchangamle forest (the forest that is now gone; Nowak *et al.* [2009]) had the most unique (least similar to the other six transects) plant community assemblage including a member of the family Orchidaceae, *Vanilla roscheri.* It was also the most diverse transect in Uzi/Vundwe (88 species, 19.5 effective species, and a 2.97 Shannon Diversity Index value).

Differential habitat-use patterns of colobus and Sykes's monkeys were observed. In Kiwengwa, the pattern of habitat use by both species appeared to be preferential for high coral rag forest, whereas in Uzi, habitat use was more proportional to its availability, although a preference for medium coral rag was marked. The strongest habitat-use pattern (i.e. occurrence in high forest) was observed for colobus in Kiwengwa (Fig. 2).

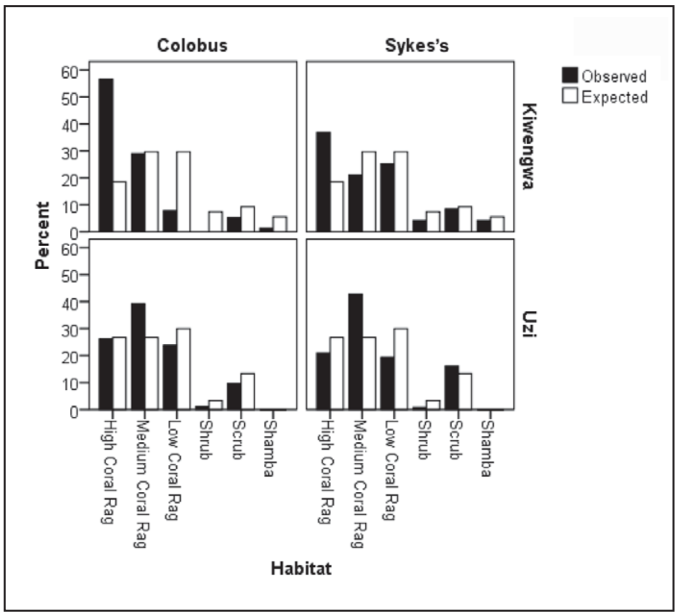

Figure 2. Percentage of observed and expected sightings of colobus and Sykes's monkeys by vegetation type and site. Shamba = cultivated land.

The higher than expected occurrence of colobus in high and medium coral rag can be attributed to the availability of colobus-preferred foods in this habitat. High coral rag in Kiwengwa and medium coral rag in Uzi had the highest sum basal area (BA) of the top ten colobus food plants. Although the mean group size of colobus was not significantly higher in medium to high canopy coral rag compared with the other vegetation types in either Kiwengwa or Uzi (t-test: Kiwengwa, -1.756, df = 74, n.s.; Uzi, 0.468, df = 174, n.s.), the maximum group sizes for colobus were recorded in medium coral rag at both sites (max in Kiwengwa = 20, mean = 6.62 ± 3.42, $n = 76$; max in Uzi = 25, mean = 6.59 ± 4.29, $n = 176$).

At both sites and across transects, higher plant species density was associated with higher colobus group density (Table 2), and the same general pattern was seen for Sykes's monkeys. The significant relationship between Sykes's monkeys and colobus food BA (Table 2) can most likely be explained by dietary overlap between the two species; their frequent use of *Ficus* spp. (e.g., *F. sur*, *F. natalensis*), for example.

Phenology

Production of plant parts differed between sites (ANOVA, $F_{1, 115} = 23.7$, $p < 0.001$) and, controlling for site, there was significant seasonality in production (ANOVA Type I model, $F_{4,115} = 3.05$, $p = 0.02$). Kiwengwa had higher overall mature leaf availability, while Uzi had more young leaves, fruits, buds and flowers (Nowak 2007). Production as well as availability (as measured by BA and density) was less variable across seasons in Uzi than in Kiwengwa, which was a more seasonal habitat with an extended period of food scarcity from September to December. There was no evidence of a relationship between colobus density and overall mature leaf availability (ANOVA, $F_{1, 27} = 15.12$, $p < 0.001$), which was higher in Kiwengwa (mean score, 8.1 ±0.39 SE) than Uzi (6.0 ±0.30 SE). A next step would be to evaluate leaf quality, a known correlate of colobus abundance (Fashing 2008).

Habitat disturbance

More humans, dogs, and humans with dogs were encountered in Kiwengwa ($n = 146, 13, 3$) than in Uzi ($n = 89, 0, 1$) ($\chi^2 = 7.81$, df = 2, $p = 0.02$). High human encounter rates

Table 2. Spearman correlations of monkey densities, human encounter rates and vegetation characteristics ($n = 7$ transects).

	Vegetation characteristics						
	Shannon Diversity Index	**Density of top 10 colobus foods**	**BA[1] of top ten colobus foods**	**Plant species density**	**Plant species BA**	**Density of cut stems**	**Total BA cut**
Red colobus	-0.64	***0.86**	0.64	****0.93**	-0.25	0.36	0.00
	n.s.	***p* = 0.014**	n.s.	***p* = 0.003**	n.s.	n.s.	n.s.
Sykes's monkeys	-0.50	0.71	***0.82**	***0.79**	-0.64	0.21	0.57
	n.s.	n.s.	***p* = 0.023**	***p* = 0.036**	n.s.	n.s.	n.s.
Humans	0.18	-0.56	-0.25	-0.23	-0.38	0.54	0.67
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s	n.s.

[1]BA = Basal area
** Correlation significant at the 0.01 level (2-tailed).
* Correlation significant at the 0.05 level (2-tailed).

Figure 3. Adult male Zanzibar red colobus *Procolobus kirkii* eating mangrove flowers on coral rag, southern Uzi Island, Zanzibar Archipelago, Tanzania. Photo by Andrew Perkin.

Figure 4. Adult male Zanzibar red colobus *Procolobus kirkii* sits on jagged coral rock formation, Vundwe Island, Zanzibar. Photo by Andrew Perkin.

tended to be associated with lower numbers of monkey sightings, with an exception in Uzi, where Sykes's monkey and human encounter rates tended to correlate, suggesting their use of relatively disturbed forest at this site (Table 2).

Both overall (r_s = 0.372, p <0.001) and in Kiwengwa, if more groups of colobus were seen, then more groups of Sykes's monkeys were seen. The other species was likely to be seen either simultaneously or at another time on the same transect in 71% of Kiwengwa and 90% of Uzi census walks. Co-occurrence between monkey species on the same transect was more likely when humans were also seen on the transect (χ^2 = 9.67, df = 1, p <0.05).

Overall, more woodcutters, dogs, and humans with dogs were encountered in medium coral rag in both sites (91 of 251 encounters). Human signs consisted mainly of cut trees, consistent with the bulk of human encounters (woodcutters), and human signs were positively associated with human encounters along the seven transects (r_s = 0.728, n = 7, p = 0.063). In Kiwengwa, many small stems were disturbed, while in Uzi disturbance to large trees was pronounced. Areas with higher human encounter rates tended to have smaller trees, while human sign in the form of historically cut tree BA was positively associated with human encounter rates. People appeared to be using the edge or re-growth forest having at some stage removed many larger trees.

After woodcutting, hunting in Kiwengwa was the second most common human activity, and although most hunting was for bushpig, duiker and guineafowl, shots and chases also flushed monkeys. In Uzi, boating/fishing was the second most common human activity and did not represent a direct threat to monkeys.

No significant relationships between disturbance measures and monkey densities were detected despite clear habitat-use patterns by monkeys.

Discussion

The results of these surveys, while conducted almost a decade ago, are suggestive of the relative value of degraded habitats to colobus and Sykes's monkeys. This value may have been elevated as a result of overall declining habitat suitability and availability on Zanzibar, and colobus and Sykes's monkeys were observed to travel through and feed in low and dense habitats (e.g., *Rhus natalensis* tangle) when moving between taller forest stands, for which they showed a preference.

The density estimates reported here act as a baseline for future, and ideally, more comprehensive, island-wide surveys of red colobus and Sykes's monkeys on Zanzibar. The sites we censused represented the second (Uzi/Vundwe) and third (Kiwengwa-Pongwe) largest populations of red colobus after JCBNP (these locations were chosen for transect surveys after visits to other parts of the island prior to establishing the study areas, as well as consultations with relevant authorities; Nowak [2007]). Colobus were encountered at a higher rate in Uzi and Vundwe islands than in Kiwengwa-Pongwe forest, where human disturbance was more frequent and dispersed, and food availability was more seasonal. In 2005, Kiwengwa and Uzi still supported populations of red colobus comparable to levels estimated by Silkiluwasha more than 30 years ago (1981) suggesting some degree of resilience to human disturbance and an ability to survive in secondary forest and at habitat edges (Onderdonk and Chapman, 2000); however, in 2011, while both species were still present at these sites, given extensive forest cutting as well as poisoning of monkeys they are presumed to have suffered significant declines (Nowak *et al.* 2009; K. Nowak, pers. obs. 2009 and 2011).

Variables other than disturbance may have contributed to observed density patterns in 2004–2005. Although colobus density estimates in Uzi were notably lower than those recorded in farm-field mosaics outside JCBNP (Siex 2003), the high density estimates in Uzi relative to Kiwengwa could have also been due to population compression. Evidence for compression (and barriers to movement) included the lack of variation in monkey densities observed across Uzi transects and between census walks relative to marked variation across Kiwengwa transects, possibly indicating wider ranging patterns and less constricted movement. Another region where population compression has occurred due to habitat loss is

Figure 5. Adult male Zanzibar red colobus *Procolobus kirkii* running along a sandy beach, Vundwe Island, Zanzibar Archipelago, Tanzania. Photo by Andrew Perkin.

Tana, Kenya, where *P. rufomitratus* lives at high densities of 165 individuals/km² (similar to the density of red colobus estimated in Uzi). The farm-field groups in Siex's study (Siex 2003), at a population density more than double of those in the Jozani groundwater forest (550 monkeys/km² compared with 235 monkey/km²), were highly unstable and living at high densities because of habitat compression rather than intrinsic growth.

The highest rate of colobus encounters, at approximately 3 groups/km (68 sightings and 90 encounters including "vocalization-only"), took place on Vundwe Island, the least human-disturbed area at the time of our study. The Vundwe population of colobus is largely isolated and we found no evidence for migration between southern Uzi and northern Vundwe; however, the island had huge potential to be a biodiversity refuge despite limits to dispersal.

Fission-fusion

One potential source of group density over-estimation was fission-fusion. This bias can be offset by reporting density as individuals/km². Siex (2003) reported that the ground-water forest groups of Jozani spent nearly 50% of their time split into two or more foraging parties, whereas the habitat-compressed shamba groups never split into subgroups. We observed a similar pattern for colobus groups in coral rag and mangrove respectively (Nowak and Lee 2011b). Fission-fusion may occur in the absence of predators and where food is scarce and clumped (Struhsaker and Leland 1979). No reports of fission-fusion in Zanzibar colobus populations other than Jozani were reported prior to this study, but fission-fusion structures have been documented in *P. gordonorum* and *P. badius badius* in heavily logged areas and areas of low food plant species diversity and density, even under risk of predation (Struhsaker 2000). Social flux in coral rag forest may be related to the observed high level of habitat degradation (consistent with the observations of Marshall *et al.* [2005] and Berenstain [1986]). As *P. badius* species rarely have group sizes of less than 10 individuals (Struhsaker *et al.* 2004; Nowak and Lee 2011b), the small mean group sizes we recorded on census suggest a habitual fission-fusion social system.

Co-occurrence of colobus and Sykes's monkeys

That Sykes's monkey sightings were positively correlated with human activity in Uzi (but not Kiwengwa) is consistent with Marshall *et al.* (2005) who found that Sykes's monkey abundance was positively related to human signs in the form of number of cut poles and timber stumps in Udzungwa Mountains, Tanzania. Cercopithecines may be more adaptable to disturbed environments and regrowth habitats than colobines (Fimbel 1994a, 1994b), but trends in Kiwengwa suggest that both species are susceptible and resilient to human disturbance. In Uzi, colobus densities were higher than those of Sykes's monkey, while no notable difference was observed in Kiwengwa, where human encounters occurred at a higher rate, vegetation was more disturbed, and the two species associated more frequently and co-occurred in the presence of humans. Unusually frequent mixed groups of *Procolobus gordonorum* and *Colobus angolensis palliatus* have been observed in areas of high human forest use in New Dabaga/Ulangambi Forest Reserve (NDUFR) in Tanzania (Marshall *et al.* 2005), suggesting that interspecific associations may increase in areas of anthropogenic disturbance or other mortality risks.

The value of unprotected areas for the future conservation of Zanzibar red colobus, and sympatric Sykes's monkeys, probably remains high, but enforcing protection of a legally protected species in unprotected areas is challenging (Mbora and Meikle 2004; Davenport *et al.* 2013). As few large forests remain on Unguja other than those described in this study—Kiwengwa-Pongwe, and Uzi and Vundwe—it is reasonable to propose that the successful conservation, timely assignment of protected status, and enforcement of regulations in these two regions (listed among 62 "Priority Primate Areas" in Tanzania by Davenport *et al.* 2013) will be important to securing the survival and genetic and behavioral diversity of Zanzibar red colobus.

Acknowledgments

This study was greatly facilitated by Dr. Bakari S. Asseid and his colleagues from the Department of Commercial Crops, Fruits, and Forestry in Zanzibar. For their assistance in the field, we thank Aliy Abdul Rahman, Duncan Gillespie, Kirstin Siex, Salum Khamis, Mtumwa Simai, Iss-haka Hussein Abdulla and Mwinyi Khamis Mwinyi. For botanical expertise we are indebted to Said Fakih, Tahir Haji, and Kaj Vollessen. We thank Anthony Rylands and two anonymous reviewers for their valuable comments which greatly improved this manuscript. Fieldwork was funded by the Wildlife Conservation Society, Leakey Foundation, Primate Conservation, Inc., American Society of Primatologists, and the Leakey Trust.

References

Berenstain, L. 1986. Responses of long-tailed macaques to drought and fire in eastern Borneo: a preliminary report. *Biotropica* 18: 257–262.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations.* Oxford University Press, Oxford.

Buckland, S.T., A. J. Plumptre, L. Thomas and E. A. Rexstad. 2010. Design and analysis of line transect surveys for primates. *Int. J. Primatol.* 31: 833–847.

Ciani, A.C., L. Palentini and E. Finotto. 2001. Survival of a small translocated *Procolobus kirkii* population on Pemba Island. *Anim. Biodiv. Conserv.* 24: 15–18.

Davenport, T. R. B., K. Nowak and A. Perkin. 2013. Priority primate areas in Tanzania. *Oryx.* In press.

Fashing, P. J. 2008. Behavior, ecology and conservation of colobine monkeys: an introduction. *Int. J. Primatol.* 28: 507–511.

Fashing, P. J. and M. Cords. 2000. Diurnal primate densities and biomass in the Kakamega Forest: An evaluation of census methods and a comparison with other forests. *Am. J. Primatol.* 50: 139–152.

Fimbel, C. 1994a. Ecological correlates of species success in modified habitats may be disturbance- and site-specific: the primates of Tiwai Island. *Conserv. Biol.* 8: 106–113.

Fimbel, C. 1994b. The relative use of abandoned farm clearings and old forest habitats by primates and a forest antelope at Tiwai, Sierra Leone, West Africa. *Biol. Conserv.* 70: 277–286.

Grubb, P., T. M. Butynski, J. F. Oates, S. K. Bearder, T. R. Disotell, C. P. Groves, and T. T. Struhsaker. 2003. Assessment of the diversity of African primates. *Int. J. Primatol.* 24: 1301–1357.

Grubb, P. 2006. Geospecies and superspecies in the African primate fauna. *Primate Conserv.* (20): 75–78.

IUCN. 1990. 1990 IUCN Red List of Threatened Animals. IUCN, Gland, Switzerland and Cambridge, UK.

Larsen, D. R. 1997. Natural Resource Biometrics. University of Missouri, Columbia, MO. doi: www.snr.missouri.edu/nr3110. 2005.10.

Marshall, A. R., J. E. Topp-Jorgensen, H. Brink and E. Fanning. 2005. Monkey abundance and social structure in two high-elevation forest reserves in the Udzungwa Mountains of Tanzania. *Int. J. Primatol.* 26: 127–145.

Masoud, T. S., D. Finnie, A. B. Omar, A. U. Basha , R. G. Wild. 2003. *Zanzibar red colobus conservation strategy—a long term strategy for the survival of the Zanzibar red colobus*. Department of Commercial Crops, Fruits, and Forestry, Zanzibar: Forestry Technical Paper No. 137.

Mbora, D. N. M. and D. B. Meikle. 2004. The value of unprotected habitat in conserving the critically endangered Tana River red colobus (*Procolobus rufomitratus*). *Biol. Conserv.* 120: 91–99.

McGraw, W. S. 2005. Update on the search for Miss Waldron's red colobus monkey. *Int. J. Primatol.* 26: 605–619.

Mease, L. 2009. Survey of anthropogenic vegetation changes on Uzi and Vundwe islands: a study on deforestation and its implications for people and wildlife. Stanford University. ISP report. URL: <http://digitalcollections.sit.edu/isp_collection/758>. Accessed: 5 December 2013.

Mturi, F.A. 1991. The Feeding Ecology and Behavior of the Red Colobus Monkey (*Colobus badius kirkii*). PhD Dissertation, University of Dar es Salaam, Dar es Salaam.

Mturi, F.A. 1993. Ecology of the Zanzibar red colobus monkey, *Colobus badius kirkii* (Gray, 1968), in comparison with other red colobines. In: *Biogeography and Ecology of the Rain Forests of Eastern Africa*, J. C. Lovett and S. K. Wasser (eds.), pp. 243–266. Cambridge University Press, Cambridge, UK.

Nelson, J.T. and S. G. Fancy. 1999. A test of the variable circular-plot method where exact density of a bird population was known. *Pacific Conserv. Biol.* 5: 139–143.

Nowak, K. 2007. Behavioral Flexibility and Demography of *Procolobus kirkii* Across Floristic and Disturbance Gradients. PhD dissertation, University of Cambridge, Cambridge, UK.

Nowak, K. 2008. Frequent water drinking by Zanzibar red colobus (*Procolobus kirkii*) in a mangrove forest refuge. *Am. J. Primatol.* 70: 1081–1092.

Nowak, K. and P. C. Lee. 2011a. Consumption of cycads *Encephalartos hildebrandtii* by Zanzibar red colobus *Procolobus kirkii*. *J. East Afr. Nat. Hist.* 100: 123–131.

Nowak, K. and P.C. Lee. 2011b. Demographic structure of Zanzibar red colobus populations in unprotected coral rag and mangrove forests. *Int. J. Primatol.* 32: 24–45.

Nowak, K., A. Perkin and T. Jones. 2009. Update on habitat loss and conservation status of the endangered Zanzibar red colobus on Uzi and Vundwe Islands. Unpublished report for Department of Commercial Crops, Fruits and Forestry, Zanzibar. Primate Conservation, Inc., Charlestown, RI. URL: <http://www.primate.org/NowakPerkinJonesred_colobus.pdf>.

Oates, J. F., M. Abedi-Lartey, W. S. McGraw, T. T. Struhsaker and G. H. Whitesides. 2000. Extinction of a West African red colobus monkey. *Conserv. Biol.* 14: 1526–1532.

Onderdonk, D. A. and C. A. Chapman. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *Int. J. Primatol.* 21: 587–611.

Peres, C. A. 1999. General guidelines for standardising line-transect surveys of tropical forest primates. *Neotrop. Primates* 7: 11–16.

Roberts, D. L. and A. C. Kitchener. 2006. Inferring extinction from biological records: Were we too quick to write off Miss Waldron's red colobus monkey (*Piliocolobus badius waldronae*)? *Biol. Conserv.* 128: 285–287.

Siex, K. S. 2003. Effects of Population Compression on the Demography, Ecology, and Behavior of the Zanzibar Red Colobus Monkey (*Procolobus kirkii*). Ph.D. Dissertation, Duke University, Durham, NC.

Siex, K. S. and T. T. Struhsaker. 1999. Ecology of the Zanzibar red colobus monkey: demographic variability and habitat stability. *Int. J. Primatol.* 20: 163–191.

Silkiluwasha, F. 1981. The distribution and conservation status of the Zanzibar red colobus. *Afr. J. Ecol.* 19: 187–194.

Struhsaker, T. T. 1975. *The Red Colobus Monkey*. University of Chicago Press, Chicago, IL.

Struhsaker, T. T. 2000. The effects of predation and habitat quality on the socioecology of African monkeys: lessons from the islands of Bioko and Zanzibar. In: *Old World Monkeys*, P. F. Whitehead and C. J. Jolly (eds.), pp.393–430. Cambridge University Press, Cambridge, UK.

Struhsaker, T. T. 2005. Conservation of red colobus and their habitats. *Int. J. Primatol.* 26: 525–538.

Struhsaker, T. T. and L. Leland. 1979. Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. *Adv. Stud. Behav.* 9: 159–228.

Struhsaker, T. T. and L. Leland. 1980. Observations on two rare and endangered populations of red colobus monkeys in East Africa: *Colobus badius gordonorum* and *Colobus badius kirkii. Afr. J. Ecol.* 18: 191–216.

Struhsaker, T. T. and K. S. Siex. 1994. Zanzibar red colobus census for 1994. Unpublished report, Duke University, Durham, NC.

Struhsaker, T.T. and K. S. Siex. 1996. The Zanzibar red colobus monkey: conservation status of an endangered island endemic. *Afr. Primates* 2: 54–61.

Struhsaker, T.T. and K. S. Siex. 1998. Translocation and introduction of the Zanzibar red colobus monkey: success and failure with an endangered island endemic. *Oryx* 32: 277–284.

Struhsaker, T. T., A. R. Marshall, K. Detwiler, K. S. Siex, C. L. Ehardt, D. D. Lisbjerg and T. M. Butynski. 2004. Demographic variation among the Udzungwa red colobus (*Procolobus gordonorum*) in relation to gross ecological and sociological parameters. *Int. J. Primatol.* 25: 615–658.

Authors' addresses:
Katarzyna Nowak, Department of Zoology and Entomology, University of the Free State, Qwaqwa, Phuthaditjhaba, 9866, RSA, and Department of Anthropology, Durham University, Dawson Building, South Road, Durham, DH1 3LE, UK, and **Phyllis C. Lee**, Behaviour and Evolution Research Group, Psychology, School of Natural Sciences, University of Stirling, Scotland FK9 4LA, UK. E-mail of first author: <katarzyna.nowak@durham.ac.uk>.

Submitted for publication: 24 March 2013
Revised: 2 December 2013