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Protective Status, Ecology and Strategies for Improving Conservation of *Cercocebus sanjei* in the Udzungwa Mountains, Tanzania

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Sanje mangabeys (Cercocebus sanjei)*, first described in 1981, are among the most endangered primates in the world. They are endemic to the Udzungwa Mountains of Tanzania, in a biogeographic region designated one of the world's biodiversity hotspots. Conservation research since 1997 has documented the presence of the mangabey in only 3 of the relict montane forest blocks of the Udzungwas. The total population, possibly <1,500 animals, is fragmented and not adequately protected. A substantial proportion (perhaps 40%) live in forest reserves outside the protective confines of the Udzungwa Mountains National Park, and they are affected by habitat loss and hunting. Efforts to improve their conservation status include assessment of distribution, relative abundance, and habitat quality, and initiation of observational research with habituated individuals to acquire critically important data on their habitat requirements, diet, movement patterns, socioecology, and community ecology. These interrelated research activities should contribute to effective management for conservation, provide baseline information to support current efforts to expand the boundaries of the national park, and guide potential future establishment of corridors between the major forests known to support mangabey groups.*

KEY WORDS: *Cercocebus*; Sanje mangabey; Udzungwa Mountains; conservation; biodiversity hotspot; Tanzania.

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Cercocebus sanjei, one of the world's most endangered primates, is endemic to the Udzungwa Mountains of south-central Tanzania. These mountains are an important component of a larger biogeographic area, the Eastern Arc Mountains, known for its species richness and high levels of endemism. As such, preservation of Sanje mangabeys may be enhanced via research and global conservation attention which is being focused on this critical biodiversity area. However, the future of the Sanje mangabey's fragmented and highly restricted population is far from certain, and its effective conservation will require both continued research and improvement in the protective status of the very few montane forest areas where they remain.

We 1) provide an overview of the conservation significance and characteristics of the biodiversity hotspot that includes Sanje mangabeys as one of its important endemics; 2) document the mangabey's fragmented distribution and provide some assessment of their abundance; 3) provide preliminary ecological information for this virtually unstudied primate; and 4) delineate the conservation concerns evident in the Udzungwa Mountains that impact the potential survival of Sanje mangabeys, with associated recommended conservation strategies and activities.

The Biogeographic Context

A recent strategy directed toward improving conservation efficacy has been the application of the concept of biodiversity hotspots. A set of 25 biogeographic areas constitute only *ca*. 1.4% of Earth's land mass, yet they contain *ca*. 62% of the planet's vascular plant and nonfish vertebrate biodiversity. They have also undergone exceptional loss of habitat, amounting to >75% of their original vegetative cover (Mittermeier *et al.*, 2000; Myers *et al.*, 2000). One of the most important Global Biodiversity Hotspots is the Eastern Arc Mountains and Coastal Forests of Tanzania and Kenya Biodiversity Hotspot, which, despite its relatively small size, ranks first among the 25 in the number of endemic plant and vertebrate species per unit area (Myers *et al.*, 2000). This concentration of endemics also translates into recognition that it is the hotspot most vulnerable to the greatest degree of plant and vertebrate extinction for a given loss of habitat (Brooks *et al.*, 2002).

The Eastern Arc Mountains (3°20′–8°45′S; 35°37′–38°48′E) of the hotspot extend *ca*. 900 km south-southwest from the Taita Hills of southeast Kenya, southward through Tanzania, and include the Pare, Usambara, Uluguru, Nguru, Nguu, Ukaguru, Rubeho (Usagara), Udzungwa, and Mahenge Mountains as major forested sites (Figure 1). These crystalline block fault mountains and their forests are of great age, forming some 25–100 million years ago (Hamilton, 1989; Griffiths, 1993), and are

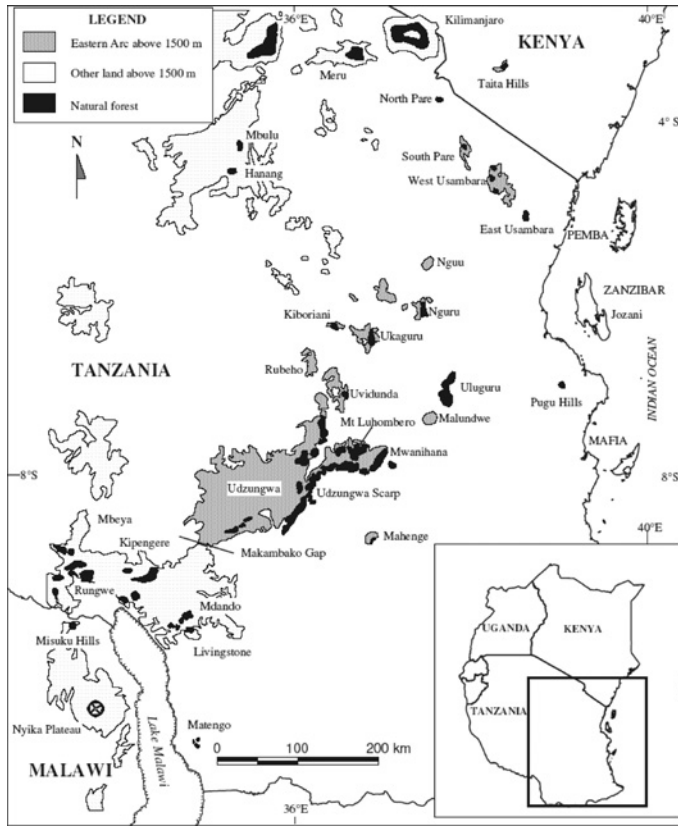

Fig. 1. Major Eastern Arc montane blocks, with distribution of land above 1500 m and areas of natural montane forest indicated. Map adapted from Stuart *et al*. (1993).

characterized by ecoclimatic stability due to persistent Indian Ocean monsoon influences bringing relatively high and reliable rainfall to the east-facing slopes (Lovett, 1990, 1993). The disjunctive montane forests have been shielded from recurrent dry periods throughout the Pleistocene which led to loss of extensive regions of forest elsewhere in East Africa (Axelrod and Raven, 1978). Lovett and Friis (1996; Lovett, 1998a,b) hypothesized that this environmental stability over evolutionary time-scales has resulted in both the survival of relict taxa and in the generation of new ones, leading to the extreme degrees of endemism and species richness that characterize this montane region. For example, >30% of the >2000 moist forest plant species are endemic (Lovett, 1988, 1993), and in terms of restricted-range bird species, the mountains are ranked as the 2nd or 3rd most important

area in Africa for conservation (Dinesen *et al.*, 1993; Butynski and Ehardt, 2003). These statistics are even further accentuated when it is recognized that a number of forests in the Eastern Arc Mountains remain unsurveyed, large numbers of collected species have yet to be identified, and new taxa are recorded from the mountains annually.

The natural forests of the Eastern Arc Mountains are highly fragmented. Although the total area of natural forest may be in the range of 5340 km^2, only *ca.* 1447 km^2 (27%) is closed canopy, and forest sizes are small: median forest size is 10.2 km^2; mean forest size is 58.0 km^2 (Newmark, 1998). Approximately 77% of the original forest cover has been lost during the past 2000 years, due to human disturbance and fires, with most of that occurring in the last 200 yr (Newmark, 1998). This significantly impacts conservation of the endemic and rich flora and fauna, given that what remains of the forest cover is highly fragmented, many of the species have extremely restricted ranges, and a large number of the fauna will not cross forest gaps, prohibiting dispersal and limiting population viability. Significant human impact continues in the Eastern Arc Mountains, and, as pointed out by Lovett (1998a), the fact that many of the endemic species are present due to the environmental stability of the region makes them especially fragile with respect to perturbations in their habitats.

The Udzungwa Mountains (7°40′–8°40′S; 35°10′–36°50′E) are the southernmost and largest of the Eastern Arc Mountains. From a biodiversity standpoint, they are arguably the most important mountains in the region, if not the most important in East Africa (Rodgers and Homewood, 1982; Jensen and Brøgger-Jensen, 1992; Butynski *et al.*, 1998; Dinesen *et al.*, 2001). Extending roughly 200 km northeast/southwest and covering an area of *ca.* 10,000 km^2, they are unusual in that the eastern escarpment exhibits continuous forest zonation from 300–2250 m a.s.l., ranging from lowland forest in the Great Ruaha River Valley, through mid-altitude *Parinari* rain forest, to montane forest of *Podocarpus/Hagenia/Prunus* and bamboo at the higher elevations (Rodgers and Homewood, 1982; Butynski and Ehardt, 2003). The Udzungwas contain the largest area of natural and closed forest and the largest number of forests ($n = 26$; Newmark, 1998) in the Eastern Arc Mountains, and the species composition is diverse, both within and between forests. The majority of the forests are <25 km^2. (Newmark, 1998), interspersed with large areas of grassland and some woodland, and laced with numerous rivers and streams; mean annual rainfall along the southeastern scarp is *ca.* 2000 mm, decreasing to 900 mm on the western plateau. They harbor the largest number of endemic and near-endemic species of birds in the Eastern Arc Mountains, some of which are threatened, and they are second only to the East Usambara Mountains (by 1 taxon) in number of endemic and near endemic mammals

(Burgess *et al.*, 1998a). This rich biodiversity, characterized by high degrees of endemism, led to the establishment of the Udzungwa Mountains National Park (UMNP) in 1992, a protected area of 1990 km^2 and the first in Tanzania to be established primarily for conservation of biodiversity. However, the park encompasses only some of the forests in the Udzungwas (Figure 2); the other very significant forests are currently classified as Catchment Forest Reserves and suffer substantially from detrimental activities such as illegal agricultural encroachment, logging, and hunting.

It is solely within the Udzungwa Mountains forests that the severely limited and fragmented remaining population of one of the world's 25 most endangered primates (Konstant *et al.*, 2002) *Cercocebus sanjei*, lives. As a significant part of a more generalized conservation project focused on the primates, birds, and larger mammals of the Udzungwas, and via interrelated activities, we have been assessing their distribution and abundance, and attempting to merge scientific investigation with conservation policies, strategies, and management in an effort to insure their survival (Butynski *et al.*, 1998; Ehardt *et al.*, 1999; Ehardt, 2001; Butynski and Ehardt, 2003; Struhsaker *et al.*, 2004). Here we summarize our major findings. General efforts to conserve the important forests of the Udzungwas will certainly contribute to conservation of Sanje mangabeys, though substantial research and conservation policy must also be specifically directed toward the remaining mangabey population if the taxon is to survive.

Current Knowledge about Sanje Mangabeys

The Udzungwas are Tanzania's most important area for primate conservation. Sanje mangabeys share the forests with 5 other species of anthropoid primates and probably 3–5 species of galagos. The diurnal monkeys include 2 endemic taxa: *Cercocebus sanjei* (Endangered, IUCN, 2003) and *Procolobus gordonorum* (previously classified as Endangered, now listed as Vulnerable; Baillie and Groombridge, 1996; IUCN, 2003). Also present are *Colobus angolensis palliatus* (Data Deficient; IUCN, 2003), *Cercopithecus mitis* ssp., *Cercopithecus aethiops rufoviridis*, and *Papio cynocephalus cynocephalus*. The forest-dwelling galagos include *Galagoides orinus* (Data Deficient; IUCN, 2003), and *Galagoides zanzibaricus*, until recently thought to be an endemic taxon to the Udzungwas and designated *Galagoides udzungwensis*, though now recognized as a population of the more widespread Zanzibar dwarf galago (Lower Risk/Near Threatened; IUCN, 2003). *Otolemur crassicaudatus* and probably *Galago senegalensis* occur in the drier rain shadow of the Udzungwa escarpment, and our survey work suggests the possible presence of *Galagoides grantii*, though this remains unconfirmed.

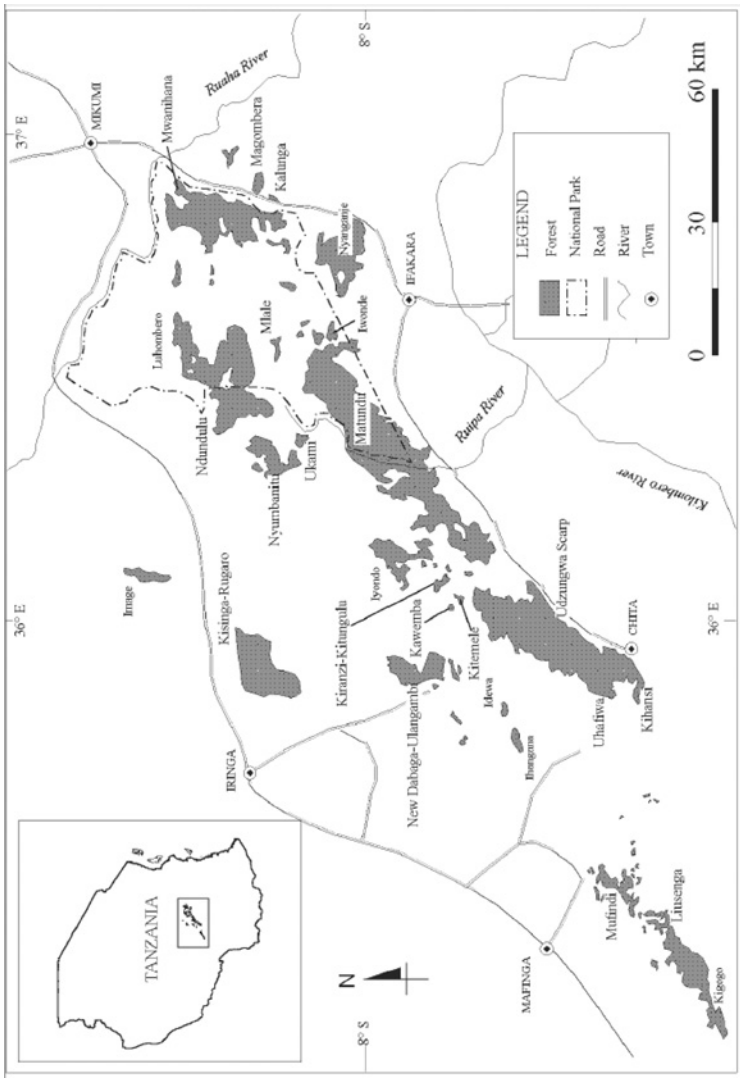

Fig. 2. Distribution of forests in the Udzungwa Mountains and indication of the current boundaries of the Udzungwa Mountains National Park. The West Kilombero Forests comprise the Luhombero, Ndundulu, Nyumbanitu, and Ukami Forests. Map adapted from Dinesen (1998).

Sanje mangabeys, first described by Homewood and Rodgers in 1981, were classified as a subspecies of *Cercocebus galeritus* (*C. g. sanjei*), though current authorities indicate that specific status is warranted (Kingdon, 1997; Groves, 2001). They probably are closest taxonomically to *Cercocebus galeritus*, and they certainly belong to the mangabey clade that is closest to *Mandrillus* within the Papionini, and are distinct from *Lophocebus*, which has affinity with *Papio* and *Theropithecus* (Harris and Disotell, 1998; Fleagle and McGraw, 1999). Our preliminary observations indicate that, consistent with their phylogenetic status, Sanje mangabeys share the ecological adaptation for feeding on seeds, nuts, and invertebrates on the forest floor (in addition to fruit) that also characterizes other *Cercocebus* spp. and *Mandrillus* (Homewood and Rodgers, 1981; Hoshino, 1985; Wasser, 1993; Rogers *et al.*, 1996; Ehardt *et al.*, 1999; Fleagle and McGraw, 1999; Ehardt, 2001; Shaw, 2003).

Distribution and Conservation Status

Between 1997 and 2002, we conducted surveys of the primates in forests within UMNP and in the major catchment forest reserves surrounding the park. We moved slowly (*ca.* 1 km h^{-1}) through the forests along animal trails or cleared pathways, camping virtually every night in a different area of the forest, and recording all primates seen or heard (the latter on the basis of species specific loud calls or other vocalizations). Standardized transect walks are extremely difficult due to the steep and often inaccessible terrain. When primates were encountered, we determined group sizes if possible, but most observations included only species records (single and interspecific associations), location, altitude, and time. The characteristic whoop-gobble loud call of mangabeys can be heard at distances of $\leq$1 km, permitting a significant number of records beyond actual sightings. As the whoop-gobble is most frequently given in the early morning and late afternoon, we often positioned ourselves at these times on ridges flanked by valleys to listen for and to locate different mangabey groups.

Our surveys, when combined with that of other researchers (Dinesen *et al.*, 2001), indicate that there are <1500 mangabeys and the population is fragmented across 3 of the 26 disjunctive Udzungwa forests (separated by expanses of fire-maintained grassland). Within the UMNP, we found mangabeys only in the Mwanihana Forest (300–2080 m a.s.l.; 7°40′–7°57′S, 36°46′–36°56′E; ~131 km^2 closed forest: Burgess *et al.*, 1998b; Figure 3), despite intensified efforts in the last few years to find them in the forest surrounding Mt. Luhombero in the western region of the park, the only other site in UMNP that might have mangabeys. Of paramount concern is that $\leq$40% of the remaining population of Sanje mangabeys lives in

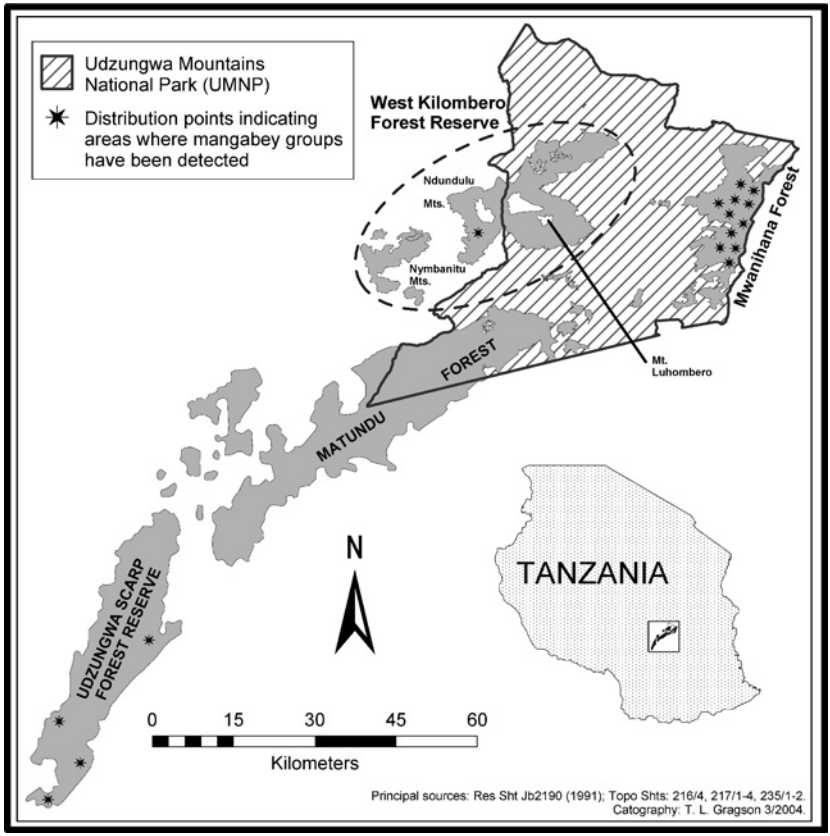

Fig. 3. Major forests in the Udzungwa Mountains and distribution of Sanje mangabeys across the 3 forests in which they occur: Mwanihana Forest within UMNP, the Ndundulu Mountains of West Kilombero Forest Reserve, and Udzungwa Scarp Forest Reserve.

the Udzungwa Scarp Forest Reserve (300–2068 m; 7°39′–7°51′S, 35°51′–36°02′E; ~100 km^2 closed forest: Burgess *et al*., 1998b) and possibly in a very restricted area of West Kilombero Forest Reserve referred to as the Ndundulu Mountains (entire Forest Reserve: 1350–2500 m; 7°39′–7°51′S, 36°27′–36°42′E; ~180 km^2 closed montane forest: Burgess *et al.*, 1998b; Figure 3), where levels of protection from hunting, habitat degradation, and habitat loss are poor versus UMNP. The largest area of the historical extent of West Kilombero Forest Reserve now falls within the UMNP; it is the forest surrounding Mt. Luhombero, in which we located no mangabeys. Within the Ndundulu Mountains portion of the Forest Reserve (located outside of UMNP; ~51 km^2 of forest; Figure 3), our surveys indicated that the

subpopulation there may be extremely small, or perhaps even no longer present. Ornithologists working in the Ndundulu Mountains in the 1990's reported 4 mangabey groups in their study area (Dinesen *et al.*, 2001). However, during our more recent surveys we detected no mangabeys in the Ndundulu Mountains, nor did other researchers who conducted surveys along 2 census transects in the eastern part of the mountains (Marshall *et al.*, in prep.). It is also the stated perception of local Tanzanians that mangabey presence has declined in the Ndundulu Mountains since 1994 (Ehardt, 2001).

Table I is a summary of all published accounts on mangabey abundance and distribution and our findings. We conclude that based both on relative abundance and level of protection, Mwanihana Forest in UMNP is the most important area of the Udzungwas for conservation of Sanje mangabeys. Estimates of population size for Mwanihana mangabeys have been attempted by previous observers, though their calculations were based on very cursory information, are difficult to interpret, and perhaps also are characterized by calculation errors. Rodgers and Homewood (1982) distinguished only 2 or 3 mangabey groups in the 4.5 km^2 area between 400 m and 1000 m that they surveyed in lower Mwanihana Forest, resulting in an estimate of 0.6 groups per km^2. Dinesen *et al.* (2001) estimated mangabey abundance in Mwanihana Forest utilizing this figure and the only estimate of mean group size available to them ($n = 10.2$) provided by Wasser (1993). Unfortunately, the area of forest in Mwanihana (177 km^2) in their calculation is probably too large and incorporates areas without suitable habitat, such as bamboo. Their area estimate of forest greatly exceeds that of Rodgers and Homewood (1982), who reported the area of natural forest to be 59 km^2, and it is also larger than the 131 km^2 of closed forest reported by Burgess *et al.* (1998b). A further complication with the Dinesen *et al.* (2001) population estimate is their application of 0.3 groups/km^2 for elevations above 1000 m, and a differing estimate of 0.6 groups/km^2 for forest below 1000 m. Their figures are difficult to reconcile with those of Rodgers and Homewood (1982), their source for the estimates. These concerns aside, Dinesen *et al.* (2001) estimated the total population in Mwanihana to be *ca.* 800 mangabeys, with more mangabeys below 1000 m than in the higher elevation forest above 1000 m.

A possible adjustment to these population estimates would be to recalculate them on the basis of the more comprehensive evaluation of the area of closed forest in Eastern Udzungwa National Park (131 km^2) of Burgess *et al.* (1998b); Mwanihana Forest would comprise the vast majority of the area. If we apply the Homewood and Rodgers (1981) estimate of 0.6 groups/km^2 to the entire estimated forest area, and the 10.2 mean group size reported by Wasser (1993), there would be 800 mangabeys in the area.

Table I. Summary of mangabey groups detected in each forest area in the Udzungwa Mountains

Forest	Source[a]	Survey or census effort	Mangabey groups detected	Total altitudinal range covered (meters a.s.l)
Mwanihana Forest-UMNP	Rodgers and Homewood (1982)	31 days	2–3	400–1650
	Wasser (1993)	200 censuses/4trails	6	450–1050
	Ehardt *et al.*–2001 Survey	17 days	16	300–2000
	Ehardt *et al.*–Censuses	136 censuses/4 transects	11	300–800
West Kilombero FR:				
Ndundulu Mtns.	Dinesen *et al.* (2001)	379 days (during 1991–2000)	4	1400–1600
	Ehardt *et al.*	5 days	0	1250–1780
	Marshall *et al.* (in prep.)	96 hours/17 censuses/2 transects	0	1370–2090
Luhombero Forest-UMNP	Ehardt *et al.*	29 days	0	1220–2500
Udzungwa Scarp FR	Dinesen *et al.* (2001)	58 days	.2 groups/km^2	300–1500
	Ehardt *et al.*	16 days	2[b] and 1 skin[c]	400–1800

[a]Ehardt *et al.* refers to both this publication and research conducted by us and our collaborators, including Dr. Thomas T. Struhsaker.
[b]Personal communication from Thomas Struhsaker and Andrew Marshall, based on 2 days of survey above the town of Chita in the southern area of Udzungwa Scarp FR, 2003.
[c]Dried skin of an adolescent Sanje mangabey brought to camp by local villagers during a survey of the northern area of Udzungwa Scarp FR in 2000. They said that it had been killed in the area by a crowned eagle.

This estimate is equivalent to that of Dinesen *et al.* (2001) based on their larger area of forest because the estimate of groups/km^2 is not reduced for forest above 1000 m a.s.l. Our surveys do not suggest a significant reduction in relative abundance of mangabeys in forest above 1000 m, so a consistent application of 0.6 groups/km^2 seems appropriate. Although Rodgers and Homewood (1982) suggested there may be a lower density of mangabey groups in forest above 1000 m, this was based on very limited data, and contrarily, Wasser (1993) reported that mangabeys appeared to be more abundant above 1000 m in his study area.

Estimates of abundance or density are characteristically difficult and problematic in application, requiring assumptions that often may not be met (Struhsaker, 1997, 2002; Mitani *et al.*, 2000). Recognizing this, we provide 2 rough population estimates from our research in Mwanihana. The first is based on a count of the minimum number of groups detected during our survey and from more systematic, repeated censuses along 4 km transects extending into Mwanihana from 4 points along a roughly 18 km stretch of the eastern boundary of UMNP. The latter provide information on the number of groups in the lower parts of Mwanihana, whereas the survey data are concentrated in the more western and higher elevations of Mwanihana. Along the 4 census transects, $\geq$11 groups of mangabeys have been located in lower elevation forest along the southeastern escarpment. During the 2001 survey in the western portion of Mwanihana, we detected $\geq$13 groups. In addition, in the vicinity of the study site for the habituated mangabey group, there are $\geq$4 distinct groups not previously counted. Finally, $\geq$1 additional group ranges in the area of Mwanihana near the headquarters facilities for the UMNP. Accordingly, there are $\geq$29 mangabey groups in the Mwanihana Forest. Applying Wasser's (1993) mean group size estimate of 10.2, there are $\geq$300 mangabeys in Mwanihana based on our count of known specific groups. This is significantly below the estimate of Dinesen *et al.* (2001), though perhaps more empirically based in that their estimate was based on the questionable application/interpretation of information presented in Rodgers and Homewood (1982) and an inappropriate estimate of forest size. The 29 groups that we counted occur in a variety of habitats, including low-elevation miombo woodland dominated by *Brachystegia microphylla*, mosaic habitats, and mature, moist evergreen montane forest, at elevations ranging from 300 m to 1800 m a.s.l.

There are significant areas of Mwanihana Forest that were not covered in the count of 29 mangabey groups. If we estimate that they were counted in a detection area of roughly 55 km^2 (utilizing recorded locations and our movements plotted on topographic maps), or *ca.* 42% of the estimated 131 km^2 of closed forest, there may be *ca.* 69 mangabey groups in

Mwanihana. Application of the 10.2 mean groups size would then yield a rough estimate of 700 mangabeys in the eastern closed forest of UMNP.

A second approach to population estimation is to count the number of 1 km^2 blocks (delimited on 1:50,000 topographic maps of the area) covered during our 2001 survey of Mwanihana (based on GPS readings at locations of camps and observations of primates) and use it as a base for calculating groups detected per km^2 surveyed. We covered $\geq$36 km^2 of forest in the 17-day survey, and detected $\geq$16 mangabey groups, resulting in an estimate of 0.44 groups/km^2. Applying Wasser's (1993) mean group size of 10.2 gives an estimate of 595 mangabeys in the roughly 131 km^2 of closed forest in eastern UMNP, which is very consistent with that derived on the basis of the likely detection area covered by the repeated censuses along the 4-km transects across the eastern area of Mwanihana. If we consider the area covered by the censuses to be 24 km^2, detection of 11 mangabey groups produces an estimate of .46 groups/km^2 and a population estimate of 600 individuals in the total area of closed forest.

The mean group size of 10.2 in our calculations may be an underestimate, perhaps seriously so. Preliminary observations of the habituated study group indicate that mangabey groups are disassociating into $\geq$2 subgroups, which may persist for as long as 6 h before regrouping. This behavior may have contributed to the low group size counts incorporated into Wasser's (1993) calculation, given that he reported a range of 1–40 mangabeys per group ($n = 6$ groups). Wasser also indicated that his methodology probably resulted in underestimates of mean group sizes for all of the primates in his study area. The habituated group in Mwanihana currently has 40 members, and minimum counts from 3 other mangabey groups in the study area range from 2 to 36, with a mean of *ca.* 14. Minimum counts by Ehardt (1994) in the area previously surveyed by Wasser (1993) produced a mean of 15 mangabeys per group ($n = 13$ sightings), and Dinesen *et al.* (2001) also report a mean group size of 15 for the 4 groups they observed in the Ndundulu Mountains area, which they referred to as Luhombero Forest. A mean of the 4 estimates would be *ca.* 13.6 individuals per group. Applying this mean value to the minimum number of groups detected in Mwanihana (29) results in a minimum estimate of $\geq$395 mangabeys, and an estimate of 940 mangabeys for the projected 69 possible groups in the forest. If this recalculated mean group size is applied to the estimate of 0.44 groups/km^2, there may be $>$785 mangabeys in the 131 km^2 of closed forest in eastern UMNP.

When these various approaches to population estimates for Mwanihana are combined and stated as a range, we can conclude that between 600 and 900 mangabeys may be present in this UMNP forest. Taking into account the problems inherent in estimating abundance, we

believe that this range represents an estimate that is both reasonable and conservative, based on the research to date.

Rough population estimates for the other 2 forest areas in the Udzungwas where mangabeys have been reported to occur are provided by Dinesen *et al.* (2001). They conservatively estimate 230 mangabeys in the Ndundulu Mountains area (based on 0.3 groups/km^2 in 51 km^2 of forest and a mean group size of 15), an estimate which is probably too large given the inability to detect mangabeys in Ndundulu in recent surveys. For Udzungwa Scarp Forest Reserve, their rough estimate is 330 individuals, utilizing a measure of 160 km^2 of forest, 0.2 groups/km^2, and a mean group size of 10.2. To make this estimate for Udzungwa Scarp Forest Reserve more comparable to that for Mwanihana, it can be recomputed using the decreased estimate of 100 km^2 of closed forest presented in Burgess *et al.* (1998b). This results in a lower estimate of 200 individuals using the 10.2 mean group size, or roughly 270 mangabeys if the mean group size is 13.6 animals.

These population estimates should be used with extreme caution. Estimates of the area of suitable forest habitat for the mangabeys will remain inadequate until mapping, combined with ground-truthing, is completed, and until further research defines the mangabey's habitat requirements. In addition, counting of subgrouping as groups could bias the number of groups detected, especially when based on vocalizations, though it also is certain that surveys do not detect all groups in an area.

Even with recognition of the problematic nature of these various population estimates, two conclusions are warranted. First, it is unlikely that the entire remaining population of mangabeys exceeds 1500 individuals, and it may be substantially less and even declining, at least in the Ndundulu Mountains. Further, the small population is fragmented across $\leq$3 disjunctive forests, each of rather small area. As such, the potential for dispersal, given the extent of nonforest habitat between the subpopulations, is very limited. Summing the estimated areas of closed canopy forest for the 3 forest areas (*ca.* 131 km^2 for Mwanihana, *ca.* 100 km^2 for Udzungwa Scarp Forest Reserve, and *ca.* 51 km^2 for the Ndundulu Mountains portion of West Kilombero Forest Reserve), the entire fragmented population of Sanje mangabeys is restricted to $<$300 km^2 of forest, only *ca.* 45% of which is within the relatively well-protected UMNP.

Preliminary Data on the Mangabey's Conservation Ecology/Socioecology

Effective conservation begins with and relies upon sound, comprehensive ecological knowledge about threatened species. In the present global context, there is urgent need for research that contributes to our understanding of primates living in insular, fragmented environments, as well as

data that allow us to evaluate the demographic, ecological and social parameters that determine extinction risk in endangered species. Although some primates are severely affected by habitat alteration and its sequelae (Johns, 1985, 1986; Skorupa, 1986; Grieser Johns and Grieser Johns, 1995; Struhsaker, 1997), others can tolerate limited or specific forms of habitat modification such as light or selective logging (Skorupa, 1986; Johns and Skorupa, 1987; Oates *et al.*, 1990; Wilkie and Finn, 1990; Johns, 1991; Thomas, 1991; Weisenseel *et al.*, 1993; Struhsaker, 1997). What we do not adequately understand are the aspects of primate ecology and demography that permit some taxa to persist while others decline, and we have not evaluated the limits to ecological flexibility in primates that have the ability to survive under conditions of fragmentation or other forms of habitat alteration. For endangered primates, such as Sanje mangabeys, it is critical to understand their adaptability and, very importantly, the limits to their flexibility, questions which can be addressed through population ecology and socioecological research in the Udzungwa forests.

Research on primates residing in altered and limited environments has begun to delineate the important ecological/socioecological characteristics and demographic aspects of particular taxa (contextualized within habitat parameters) that may contribute to predicting survival of threatened species, especially under low-population conditions characterizing primates like the Sanje mangabey (Cowlishaw and Dunbar, 2000). Potential (and often interrelated) predictors of population viability include specific diet (type, diversity, breadth, and flexibility); group size, composition, and fluidity (fission-fusion capacity); range size; degree of terrestriality; dispersal ability, including ability to utilize/cross environmental matrices; potential to use secondary forest, including seasonally; conspecific group responses to one another, especially under conditions of resource variability; and degrees of interspecific competition, including niche separation and overlap in keystone resources (Wilson and Johns, 1982; Johns and Skorupa, 1987; Rylands and Keuroghlian, 1988; Johns, 1991; Thomas, 1991; Fimbel, 1994; Tutin *et al.*, 1997b; Harcourt, 1998; Onderdonk and Chapman, 2000). However, these characteristics of primate species and populations must be contextualized within and analyzed in conjunction with the habitat characteristics of the taxon's range. These include environmental parameters such as age, area, and degree of isolation of occupied forests (Rylands and Keuroghlian, 1988; Schwartzkopf and Rylands, 1989; Estrada and Coates-Estrada, 1996; Laurance and Bierregaard, 1997; Olupot, 1998); aspects of forest structure (Schwartzkopf and Rylands, 1989; Medley, 1993; Tutin *et al.,* 1997a; Chapman and Chapman, 1999; Tutin, 1999; Mbora, 2003; Wieczkowski, 2003), including floristic composition, e.g., plant species diversity; degree and type of habitat modification and their secondary effects,

e.g., edge effects, removal of key resources directly or indirectly (Rodgers and Homewood, 1982; Kinnaird, 1992; Lawes, 1992; Struhsaker and Siex, 1996); and presence of keystone resources, which tend to be species-specific to a large degree (Oates, 1986; Skorupa, 1986; Peres, 1991; Butynski and Mwangi, 1994; Stevenson, 2001) . With respect to Sanje mangabeys, the reality is that, at present, we have essentially no systematic information on either the ecological/socioecological/demographic characteristics of the primate or the parameters of the forests it occupies. To counter this critical absence, our research has recently progressed to collection of these essential data.

In the past year, we habituated a study group of mangabeys in Mwanihana Forest within UMNP and initiated data collection focused on their ecology. We are also assessing actual abundance of the species in the forests it occupies occupy and determining group size and composition in relation to habitat quality. The literature on primate vulnerability indicates that the risk of extinction for Sanje mangabeys is elevated due to small geographic range, fragmented population, low population density, and notable body mass. Vulnerability may also be associated with a largely frugivorous diet, large home range, increased exposure to predation, and intense competition—all factors which may be evident in their ecology. Alternatively, if our initiated research demonstrates significant ecological flexibility in aspects of diet, grouping patterns, and use of environmental matrix, as is true for closely related Tana River mangabeys (Homewood, 1976; Kinnaird, 1990; Wieczkowski, 2003); availability of keystone resources in sufficient amount and diversity to support the mangabeys during seasonal lows in food resources; ability to utilize secondary forest in a significant portion of the mangabey's range, e.g., due to the logging, which occurred in the 1960s and 1970s in the lower elevations of Mwanihana Forest; and dispersal capacity across environmental matrices with ability to utilize mosaic environments, one might predict enhanced population viability.

With respect to ecological data, virtually nothing is known of Sanje mangabey habitat requirements, diet, movement patterns (ranging and dispersal), social structure, or aspects of social organization such as mating patterns. The initial information that we have is from Wasser's (1993) research, which was not specifically focused on the mangabey. It suggests that Sanje mangabeys may be largely frugivorous (>60% of observed plant parts eaten), though possibly flexible in their diet, and they may have large home ranges. The only other information is a consequence of our opportunistic observations during previous research on Udzungwa primates (Ehardt *et al.*, 1999; Ehardt, 2001), and preliminary data from the ongoing study of the habituated grow by Ehardt and Jones.

Although systematic study of mangabey ecology is only in initial phases, the following summary of our preliminary, nonsystematic observations provides some indication of their potential viability in relation to the predictive parameters outlined above.

Although Sanje mangabeys utilize resources from all strata of the forest, the group spends significant amounts of time (*ca.* 51% daily) foraging on the ground and in the lower levels of understorey trees and shrubs (<10 m above ground), including digging out roots of plants such as *Costus* sp. from 50 cm below the surface. Early mapping of habitat use indicates a home range that overlaps that of 2 other mangabey groups and encompasses ≥200 ha of very diverse habitat. The incompletely documented home range area is expected to increase as the study group appears to alter their movement patterns with seasonal fluctuation in resource availability across this mosaic habitat. The study group has 40 members; social structure is multimale (4 adult males present); solitary adult males occur; and the group regularly fissions into ≤3 smaller foraging parties for ≥6 h, then regrouping in the evening before entering sleeping trees. As indicated by the preliminary list of food items in Table II, diet composition is diverse, encompassing fruit pulp, seeds, nuts, flowers, mature and young leaves, young shoots, roots, gum, bark, lichen, tree ferns, fungi, and invertebrates from epiphytes on trees and from decomposing wood on the forest floor.

During their daily activities, the mangabeys regularly associate (*ca.* 28% of sightings) with ≥1 of the other 3 diurnal primate species: Sykes' monkeys, Udzungwa red colobus, and black-and-white colobus. Of the well-established associations (same tree, intermingled), 52% have involved Sykes' monkeys, a frugivore and potential competitor, though 54% of the observations were between a single adult male Sykes' monkey and the mangabey group. Twenty-eight percent of the observed associations have been with the red colobus, including observation of mangabeys grooming red colobus that have descended to the forest floor, and 20% with the black-and-white colobus. The frequent formation of polyspecific associations among Udzungwa primates has been hypothesized to relate to the potentially significant predation threat from crowned eagles (*Stephanoaetus coronatus*), which are common in the Udzungwas (Wasser, 1993; Ehardt *et al.*, 1999; Struhsaker *et al.*, 2004), and leopards (*Panthera pardus*), whose spoor we regularly observed in the study area. Attacks by eagles occur, and an adult male mangabey killed a crowned eagle during an attack on another mangabey group (Laurent *et al.*, in prep.).

If the recently initiated systematic research continues to show significant breadth and flexibility in aspects of Sanje mangabey ecology such as

Table II. Initial and incomplete list of food plants and parts consumed by mangabeys in the study area during preliminary observations

Family	Species	Part eaten[a]	Form[b]
Agavaceae	*Dracaena mannii*	Sh	T
Annonaceae	*Annona senegalensis*	Fr	T
Apocynaceae	*Tabernaemontana pachysiphon*[c]	Fr, L, G	T
Apocynaceae	*Voacanga africana*	Fr	T
Apocynaceae	*Saba comorensis*	Fr	C
Chrysobalanaceae	*Parinari excelsa*	N, Fr, L	T
Connaraceae	*Agelaea pentagyna*	Fr	T
Cucurbitaceae	*Coccinia sp.*	Fr	C
Euphorbiaceae	*Bridelia micrantha*	Fr	T
Flacourtiaceae	*Dovyalis sp.*	Fr	T
Gentianaceae (Loganiaceae)	*Anthocleista grandiflora*	Fr	T
Guttiferae	*Harungana madagascariensis*	Fr, G	T
Icacinaceae	*Rhaphiostylis beninensis*	Fr, L	C
Mimosaceae	*Albizia gummifera*[c]	Fr, S, L	T
Mimosaceae	*Parkia filicoidea*[c]	Fr, S	T
Moraceae	*Antiaris toxicaria*	Fr	T
Moraceae	*Ficus sur*	Fr	T
Moraceae	*Ficus sp. 1*	L	T
Moraceae	*Ficus sp. 2*	L	T
Moraceae	*Treculia africana*	Fr, S	T
Piperaceae	*Piper sp.*	Sh	T
Rubiaceae	*Lagynias sp.*	Fr, Fl, L	T
Rubiaceae (Rutaceae)	*Toddalia asiatica*	Fr, S, L	C
Ulmaceae	*Celtis sp.*	Fr, L	T
Verbenaceae	*Vitex doniana*	Fr, P	T
Zingiberaceae	*Aframomum sp.*	Sh	H
Zingiberaceae	*Costus sp.*	R, Fl	H

Note. Additional observations include at least 5 species of fungi and an arboreal fern, not yet identified. Final specific verifications will rest on full botanical study of collected specimens.
[a]Fl = flower; Fr = fruit (pulp); G = gum; L = leaf; N = nut; P = petiole; R = root; S = seed; Sh = shoot.
[b]C = climber; H = herb; T = tree.
[c]Plants also recorded in the mangabey diet by Wasser (1993).

diet, grouping patterns, and use of environmental matrix, this might predict enhanced population viability, despite the parameters that could characterize them and negatively affect their survival in the Udzungwas. There is reason to expect this to be the case based on existing studies of other *Cercocebus* spp. Although our observations here are preliminary, there are indications of similarity with other *Cercocebus* spp. in some important characteristics that may promote their survival. The subgrouping that we have observed also occurs in *Cercocebus galeritus* (Homewood, 1978; Kinnaird, 1990), *C. torquatus* (Mitani, 1989), and *C. agilis* (Quris, 1975; Shah, 2003),

while *C. galeritus* also exhibits supergrouping (temporary associations between different groups) under particular conditions of food distribution and abundance (Homewood, 1978; Kinnaird, 1992). The flexibility in grouping patterns may well characterize the genus and permit them to respond effectively to both scarcity and increased abundance of major food sources (Homewood, 1978; Mitani, 1989; Kinnaird, 1990; Shah, 2003). In contrast, *Lophocebus* mangabeys do not exhibit the same degree of variation in grouping patterns (Waser, 1975; Shah, 2003), whereas *Mandrillus*, a close phylogenetic relative of *Cercocebus*, exhibits remarkably large groups and evidence of frequent subgrouping (Abernethy *et al*., 2002).

The similarities among *Cercocebus* spp., and between *Cercocebus* and *Mandrillus*, also extend to their dietary composition and degree of terrestriality. Although *Lophocebus* are highly reliant on fruits and seeds (Chalmers, 1968; Waser, 1977; Wallis, 1978; Freeland, 1979; Olupot *et al*., 1998; Poulsen *et al*., 2001), they forage for them in the forest canopy. *Cercocebus* spp., in contrast, exploit both terrestrial and arboreal sources, spending significant amounts of time on the ground or in vegetation <10 m above the ground (*Cercocebus galeritus*: 51% on the ground, Homewood, 1976; *C. atys*: 80% on the ground, Range and Noë, 2002; *C. agilis*: 12–22% on the ground and 66% at 0–10 m, Quris, 1975, Shah, 2003). The proportion of fruit and seeds in the diet is consistently high (68–82% of observed time spent feeding) across studies of *Cercocebus* (Quris, 1975; Homewood, 1976; Kinnaird, 1990; Range and Noë, 2002; Shah, 2003; Wieczkowski, 2003). The specific importance of seeds, especially fallen seeds, is increasingly noted in dietary studies of *Cercocebus*, which is consistent with their dental morphology (Fleagle and McGraw, 1999), and this is coupled with an apparent predominance of monocotyledon plant parts: dietary preferences also characteristic of *Mandrillus* (Quris, 1975; Gautier-Hion, 1978; Hoshino, 1985; Lahm, 1986; Rogers *et al*., 1996; Shah, 2003; Wieczkowski, 2003). In contrast, *Lophocebus* may more strongly exploit legume seeds and dicotyledon leaves (Poulsen *et al*., 2001; Shah, 2003), and seed consumption may be a less significant part of their overall diet, at least in some areas where they have been studied (Waser, 1974; Wallis, 1978).

Conservation Concerns which Impact the Mangabey Population

There has been continuous loss of forest in the Udzungwas over the last 20 years. If Newmark's (1998) figure of 389 km^2 of closed forest present today is comparable to the 450 km^2 estimated by Rodgers and Homewood (1982) for 1981, then about 14% of the 1981 forest area has been lost over

the past two decades. Most remaining forests are small (18 of 26 forests <25 km^2; Newmark, 1998), rendering the primates and other species in the smaller forests susceptible to factors like edge effects (Murcia, 1995; Struhsaker, 1997). There is also significant concern about the serious threats to small, fragmented populations of primates, including mangabeys, from demographic and environmental stochasticity, loss of genetic diversity, and disruption of social structure and organization (Körn, 1994; Caughley and Gunn, 1996), the effects of which may not be detected immediately due to the time lags in population decline and loss for primates with extended life histories.

Despite the significant loss and degradation of the Udzungwa forests, they remain critically important to Tanzania in terms of biodiversity conservation and economic development. The forests protect vital water catchments for the lower-lying agricultural areas, especially east of the escarpment. Water flowing out of the Udzungwas supplies not only drinking water but also sustains production of sugar, rice, maize, bananas, and cassava (tens of thousands of metric tons of each produced annually in this area), and it supports teak production in the Kilombero Valley which potentially generates USD 20,000,000 in exports (Institute of Resource Assessment, 2000). The Udzungwas water catchment also feeds the rivers that generate two-thirds of Tanzania's hydroelectric power via operation of the Kidatu and Kihansi hydropower plants. Flooding and soil erosion are reduced by the Udzungwas forest cover, and the microclimate generated by the forests increases rainfall in the area.

Yet despite their biodiversity value and their economic importance, the Udzungwa forests are threatened, especially the Forest Reserves. High human birth rates and continuous immigration, especially along the eastern escarpment and fueled by economic factors, translate into annual population growth rates of nearly 3%, with some areas growing at annual rates in excess of 10%. At these rates, the human population in the region may double in the next 20 yr (Institute of Resource Assessment, 2000). Much of the immigration to the area is also a function of the presence of sufficient rainfall and good soils, environmental conditions which are rare in other parts of Tanzania. Coupled with this is concern that current community development activities will exacerbate the problem. If income generating activities, increased agricultural production, and road construction continue to be promoted in areas adjacent to UMNP and the Forest Reserves, human population densities are likely to grow at even greater rates due to increased immigration to the area. It is also highly questionable whether such community support activities (on the part of Tanzania National Parks and other organizations involved in the current community conservation

projects) are financially sustainable as population continues to grow. In contrast, the environmental education and agroforestry projects now active in the area have potential to foster conservation and not to exacerbate problems impacting the UMNP and Forest Reserves. These projects should be expanded and refined in response to research focused on the human ecology of the area, including socioeconomics, resource utilization and demography, important research which at present is too limited.

Although reasonably good protection exists in Mwanihana Forest within UMNP, we have observed agricultural encroachment, selective logging, and hunters with dogs in the Udzungwa Scarp Forest Reserve and West Kilombero Forest Reserve, as well as poachers in the western areas of the UMNP. As the human population continues to grow rapidly all around the Udzungwa Mountains, the threats to the Sanje mangabeys will increase. Accordingly, we have encouraged expansion of the boundaries of UMNP to encompass the adjacent Forest Reserves. The original proposal for the National Park had included them, but the final gazettement was much more limited due to logistical and financial concerns. Recent efforts to incorporate the important adjacent Forest Reserves garnered initial positive responses from officials within Tanzania National Parks and limited support from the Minister for Natural Resources and Tourism, but the process is convoluted, marred by competing development goals in the region on the part of certain international donors, and will take substantial time and resources if and when it becomes reality. The governmental framework for administration of forestry in Tanzania also is in flux, however, including an enhanced recognition of the biodiversity value of indigenous forests, in addition to their importance for watershed protection. Major reforms are in progress in the forest sector, including establishment of a new Tanzania Forest Service that will take responsibility for administration of the recently developed National Forest Programme (Ministry of Natural Resources and Tourism, 2001; Mariki *et al.*, 2003). If these reforms are successful, some lessening of the blatant problems of weak and ineffective oversight and supervision, lack of institutional mechanisms for biodiversity conservation, and outright corruption fostered by structural deficiencies, may be alleviated and improve conditions within the Forest Reserves. Although the new reforms are untested, we believe that conservation of Sanje mangabeys and other threatened endemics will best be secured by timely expansion of UMNP to incorporate the Forest Reserves surrounding the National Park.

A major factor affecting the survival and expansion of the Udzungwa forests is frequent extensive burning which occurs in the dry season (June-October). Local people set fires in conjunction with hunting and honey collection, or simply to keep areas open to facilitate travel (Dinesen *et al.*,

2001). Much of the grassland in the upper elevations of the Udzungwas is derived and maintained as a result of burning. Fire kills young trees in the area of expanding forest and also destroys evergreen forest areas when it enters them along ridges or via gaps along the forest edge (Fjeldså, 1999). Suppression of fire, in conjunction with re-establishment of forest corridors, is critical to increase effective population sizes and to facilitate dispersal of the forest-dependent species of the Udzungwas such as Sanje mangabeys. The placement and design of the corridors will also depend upon ecological and demographic research currently underway.

As a final point we emphasize the importance of long-term ecological monitoring to the success of conservation efforts in the Udzungwas. The initial project (Ehardt *et al.*, 1999) established the first monitoring activities in UMNP along measured and marked 4-km line transects in Mwanihana forest. Trained National Park personnel and field assistants are censusing primates and other larger mammals along them to assess the effectiveness of management and to anticipate and to resolve potential problems affecting the conservation value of Mwanihana Forest. In the absence of such ecological auditing, we have only subjective impressions of the effectiveness of conservation activities.

To be most effective, monitoring activities must obtain data on demographics, rather than simple abundance. Mwanihana Forest is critical to survival of Sanje mangabeys, and declines in their number (or other threatened taxa such as the red colobus) will be predicted from observed declines in group size, birth rate, or survivorship, even if numbers of groups remain consistent over time. Ecological monitoring is not consistently applied or effectively utilized by management in many protected areas, despite its importance for effective conservation. We hope that the long-term monitoring efforts in the Udzungwas can be sustained and provide a useful model for monitoring activities in other protected areas in Tanzania and elsewhere.

CONCLUSION

The Sanje mangabey and other primates of the Udzungwa Mountains are important components of the rich and unique faunal communities of the Eastern Arc Mountains Biodiversity Hotspot. A growing and sustained research and conservation-planning presence in the Udzungwas, which incorporates training of Tanzanians and fosters long-term ecological monitoring and the collection of data on population biology and socioecology, will contribute to their conservation. With 40% or more of the Endangered Sanje mangabeys existing in poorly protected Forest Reserves, as well as significant portions of the endemic red colobus and mountain galago populations, expansion of the boundaries of the UMNP

is now being promoted by both researchers and Tanzanian officials. If achieved, and if the area is effectively managed, the long-term conservation prospects for Sanje mangabeys will be greatly enhanced. The requisite effective management will derive from conservation policies and strategies that are fully informed by sound scientific research, including basic primate ecological and demographic research, and anthropological and economic research with the surrounding human populations. Research is currently being funded by major conservation agencies, including Conservation International, Wildlife Conservation Society, and World Wildlife Fund, with support by Tanzania National Parks and the Forestry and Beekeeping Division of the Ministry of Natural Resources and Tourism. The Udzungwas hold the most important forests for biodiversity conservation within the Eastern Arc Mountains and as such, they warrant our long-term commitment, care, and best conservation efforts.

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REFERENCES

Abernethy, K. A., White, L. J. T., and Wickings, E. J. (2002). Hordes of mandrills (*Mandrillus sphinx*): Extreme group size and seasonal male presence. *J. Zool. Lond.* 258: 131–137.

Axelrod, D. I., and Raven, P. H. (1978). Late Cretaceous and Tertiary vegetation history of Africa. In Werger, M. J. A. (ed.), *Biogeography and Ecology of Southern Africa*, Dr. W. Junk Publications, The Hague, pp. 77–130.

Baillie, J., and Groombridge, B. (1996). *IUCN Red List of Threatened Animals,* IUCN, Gland, Switzerland.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., and Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conser. Biol.* 16: 909–923.

Burgess, N. D., Fjeldså, J., and Botterweg, R. (1998a). The faunal importance of the Eastern Arc Mountains. *J. East Afr. Nat. Hist.* 87: 37–58.

Burgess, N. D., Nummelin, M., Fjeldså, J., Howell, K. M., Lukumbyzya, K., Mhando, L., Phillipson, P., and Vanden Berghe, E. (eds.) (1998b). Biodiversity and Conservation of the Eastern Arc Mountains of Tanzania and Kenya. Special Issue, *J. East Afr. Nat. Hist.* 87.

Butynski, T. M., and Ehardt, C. L. (2003). Notes on ten restricted-range birds in the Udzungwa Mountains, Tanzania. *Scopus* 23: 12–27.

Butynski, T. M., and Mwangi, G. (1994). *Conservation Status and Distribution of the Tana River Red Colobus and Crested Mangabey*. Unpublished Report for Zoo Atlanta, National Museums of Kenya, Institute of Primate Research, and East African Wildlife Society.

Butynski, T. M., Ehardt, C. L., and Struhsaker, T. T. (1998). Notes on two dwarf galagos (*Galagoides udzungwensis* and *Galagoides orinus*) in the Udzungwa Mountains, Tanzania. *Primate. Conserv.* 18: 69–75.

Caughley, G., and Gunn, A. (1996). *Conservation Biology in Theory and Practice,* Blackwell, Oxford.

Chalmers, N. R. (1968). Group composition, ecology and daily activities of free living mangabeys in Uganda. *Folia Primatol.* 8: 247–262.

Chapman, C. A., and Chapman, L. J. (1999). Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40: 215–231.

Cowlishaw, G., and Dunbar, R. (2000). *Primate Conservation Biology,* University of Chicago Press, Chicago.

Dinesen, L. (1998). Priorities for biodiversity conservation in the Udzungwa Mountains, Tanzania-based on bird data. *J. East Afr. Nat. Hist.* 87: 195–204.

Dinesen, L., Lehmberg, T., Rahner, M. C., and Fjeldså, J. (2001). Conservation priorities for the forests of the Udzungwa Mountains, Tanzania, based on primates, duikers and birds. *Biol. Conserv.* 99: 223–236.

Dinesen, L., Lehmberg, T., Svendsen, J. O., and Hansen, L. A. (1993). Range extensions and other notes on some restricted range forest birds from West Kilombero in the Udzungwa Mountains. *Scopus* 17: 48–58.

Ehardt, C. L. (2001). The endemic primates of the Udzungwa Mountains, Tanzania. *Afr. Primates* 4: 15–26.

Ehardt, C. L., Struhsaker, T. T., and Butynski, T. M. (1999). *Conservation of the Endangered Primates of the Udzungwa Mountains, Tanzania: Surveys, Habitat Assessment, and Long-Term Monitoring*. Unpublished Final Report, Margot Marsh Biodiversity Foundation, Conservation International.

Estrada, A., and Coates-Estrada, R. (1996). Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *Int. J. Primatol.* 17: 759–783.

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

Fjeldså, J. (1999). The impact of human forest disturbance on the endemic avifauna of the Udzungwa Mountains, Tanzania. *Bird Conserv. Int.* 9: 47–62.

Fleagle, J. G., and McGraw, W. S. (1999). Skeletal and dental morphology supports diphyletic origin of baboons and mangabeys. *Proc. Natl. Acad. Sci.* 96: 1157–1161.

Freeland, W. J. (1979). Mangabey (*Cercocebus albigena*) social organization and population density in relation to food use and availability. *Folia Primatol.* 32: 108–124.

Gautier-Hion, A. (1978). Food niches and coexistence in sympatric primates in Gabon. In Chivers, D., and Herbert, J. (eds.), *Recent Advances in Primatology, Volume I: Behaviour,* Academic Press, London, pp. 269–286.

Greiser Johns, A. C., and Greiser Johns, B. G. (1995). Tropical forest primates and logging: Long-term coexistence? *Oryx* 29: 205–211.
Griffiths, C. J. (1993). The geological evolution of East Africa. In Lovett, J. C., and Wasser, S. K. (eds.), *Biogeography and Ecology of the Rainforests of East Africa,* Cambridge University Press, Cambridge, pp. 9–21.
Groves, C. P. (2001). *Primate Taxonomy,* Smithsonian Institution Press, Washington, DC.
Hamilton, A. C. (1989). African forests. In Lieth, H., and Werger, M. J. A. (eds.), *Tropical Rain Forest Ecosystems. Ecosystems of the World, Vol. 14B.,* Elsevier, New York, pp. 155–182.
Harcourt, A. H. (1998). Ecological indicators of risk for primates, as judged by species' susceptibility to logging. In Caro, T. M. (ed.), *Behavioural Ecology and Conservation Biology*, Oxford University Press, Oxford, pp. 56–79.
Harris, E. E., and Disotell, T. R. (1998). Nuclear gene trees and the phylogenetic relationships of the mangabeys (Primates: Papionini). *Mol. Biol. Evol.* 15: 892–900.
Homewood, K. M. (1976). *Ecology and Behaviour of the Tana Mangabey (Cercocebus galeritus galeritus).* Ph.D. Dissertation, University College, London.
Homewood, K. M. (1978). Feeding strategy of the Tana mangabey (*Cercocebus galeritus galeritus*) (Mammalia: Primates). *J. Zool. Lond.* 186: 375–391.
Homewood, K. M., and Rodgers, W. A. (1981). A previously undescribed mangabey from southern Tanzania. *Int. J. Primatol.* 2: 47–55.
Hoshino, J. (1985). Feeding ecology of mandrills (*Mandrillus sphinx*) in Campo Animal Reserve, Cameroon. *Primates* 26: 248–273.
Institute of Resource Assessment. (2000). Socio-economic study of the Udzungwa Mountains National Park. Assessment of potential impacts of the UMNP on major agro-industrial developments in the Kilombero Valley and villages in the western side of the Udzungwa Mountains. Draft report prepared for WWF-TPO and TANAPA by the Institute of Resource Assessment (IRA), University of Dar es Salaam.
IUCN (2003). *2003 IUCN Red List of Threatened Species*. http://www.redlist.org. Downloaded March 2004.
Jensen, F. P., and Brogger-Jensen, S. (1992). The forest avifauna of the Udzungwa Mountains, Tanzania. *Scopus* 15: 65–83.
Johns, A. D. (1985). Selective logging and wildlife conservation in tropical rain-forest: Problems and recommendations. *Biol. Conserv.* 31: 355–375.
Johns, A. D. (1986). Effects of selective logging on the behavioural ecology of west Malaysian primates. *Ecology* 67: 684–694.
Johns, A. D. (1991). Forest disturbance and Amazonian primates. In Box, H. O. (ed.), *Primate Responses to Environmental Change*, Chapman and Hall, London, pp. 115–135.
Johns, A. D., and Skorupa, J. P. (1987). Responses of rainforest primates to habitat disturbance: A review. *Int. J. Primatol.* 8: 157–191.
Kingdon, J. (1997). *The Kingdon Field Guide to African Mammals,* Academic Press, London.
Kinnaird, M. F. (1990). *Behavioral and Demographic Responses to Habitat Change by the Tana River Crested Mangabey (Cercocebus galeritus galeritus).* Ph.D. Dissertation, University of Florida, Gainesville, FL.
Kinnaird, M. F. (1992). Competition for a forest palm: Use of *Phoenix reclinata* by human and nonhuman primates. *Conserv. Biol.* 6: 101–107.
Konstant, W. R., Mittermeier, R. A., Rylands, A. B., Butynski, T. M., Eudey, A. A., Ganzhorn, J., and Kormos, R. (2002). The world's 25 most endangered primates—2002. *Neotrop. Primates* 10: 128–131.
Körn, H. (1994). Genetic, demographic, spatial, environmental and catastrophic effects on the survival probability of small populations of mammals. In Remmert, H. (ed.), *Minimum Animal Populations*, Springer, Berlin, pp. 33–49.
Lahm, S. A. (1986). Diet and habitat preferences of *Mandrillus sphinx* in Gabon: Implications of foraging strategy. *Am. J. Primatol.* 11: 9–26.
Laurance, W. F., and Bierregaard, J. R. O. (1997). *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, The University of Chicago Press, Chicago.

Laurent, S., Mselewa, F., Jones, T., and Mtui, A. (in preparation). African crowned eagle *Stephanoaetus coronatus* killed by Sanje mangabey *Cercocebus sanjei*.
Lawes, M. J. (1992). Estimates of population density and correlates of the status of the samango monkey *Cercopithecus mitis* in Natal, South Africa. *Biol. Conserv.* 60: 197–210.
Lovett, J. C. (1988). Endemism and affinities of the Tanzanian montane forest flora. *Monogs. Syst. Bot. Missouri Botanical Gardens* 25: 491–496.
Lovett, J. C. (1990). Classification and status of the Tanzanian forests. *Mitteilungen aus dem Institut fur Allgemeine Botanik in Hamburg* 23A: 287–300.
Lovett, J. C. (1993). Eastern Arc moist forest flora. In Lovett, J. C., and Wasser, S. K. (eds.), *Biogeography and Ecology of the Rain Forests of Eastern Africa*, Cambridge University Press, Cambridge, pp. 33–55.
Lovett, J. C. (1998a). Importance of the Eastern Arc mountains for vascular plants. *J. East Afr. Nat. Hist.* 87: 59–74.
Lovett, J. C. (1998b). Eastern tropical African centre of endemism: A candidate for World Heritage Status? *J. East Afr. Nat. Hist.* 87: 359–366.
Lovett, J. C., and Friis, I. (1996). Some patterns of endemism in the tropical north east and eastern African woody flora. In van der Maesen, L. J. G., van Der Burgt, X. M., and van Medenbach de Rooy, J. M. (eds.), *The Biodiversity of African Plants,* Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 582–601.
Mariki, S. W., Shechambo, F., and Salehe, J. (2003). The contribution of environmental goods and services to Tanzania's economy: With reference to poverty reduction. IUCN-EARO, Nairobi.
Marshall, A. R., Topp-Jørgensen, J. E., Brink, H., and Fanning, E. (in press.) Monkey abundance and social structure in two high elevation forest reserves in the Udzungwa Mountains of Tanzania. *Int. J. Primatol.* 26: 127–145.
Mbora, D. N. M. (2003). *Effects of Forest Quality and Fragmentation on the Distribution and Abundance of the Tana River Red Colobus (Procolobus rufomitratus) in Tana River, Kenya.* Ph.D. Dissertation, Miami University, Oxford, OH.
Medley, K. E. (1993). Primate conservation along the Tana River, Kenya: An examination of the forest habitat. *Conserv. Biol.* 7: 109–121.
Ministry of Natural Resources and Tourism. (2001). National Forest Programme. Forestry and Beekeeping Division, Dar es Salaam, Tanzania.
Mitani, J. C., Struhsaker, T. T., and Lwanga, J. S. (2000). Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: Implications for conservation and census methods. *Int. J. Primatol.* 21: 269–286.
Mitani, M. (1989). *Cercocebus torquatus*: Adaptive feeding and ranging behaviors related to seasonal fluctuations of food resources in the tropical rain forest of south-western Cameroon. *Primates* 30: 307–323.
Mittermeier, R. A., Myers, N., and Mittermeier, C. G. (2000). *Hotspots. Earth's Biologically Richest and Most Endangered Terrestrical Ecosystems,* CEMEX, Mexico City.
Murcia, C. (1995). Edge effects in fragmented forests: Implications for conservation. *Trends Ecol. Evol.* 10: 58–62.
Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
Newmark, W. (1998). Forest area, fragmentation, and loss in the Eastern Arc Mountains: Implications for the conservation of biological diversity. *J. East Afr. Nat. Hist.* 87: 29–36.
Oates, J. F. (1986). African primate conservation: General needs and specific priorities. In Benirschke, K. (ed.), *Primates: The Road to Self-Sustaining Populations*, Springer, New York, pp. 21–29.
Oates, J. F., Whitesides, G. H., Davies, A. G., Waterman, P. G., Green, S. M., Dasilva, G. L., and Mole, S. (1990). Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology* 71: 328–343.
Olupot, W. (1998). Long-term variation in mangabey (*Cercocebus albigena johnstoni* Lydekker) feeding in Kibale National Park, Uganda. *Afr. J. Ecol.* 36: 96–101.

Olupot, W., Chapman, C. A., Brown, C. H., and Waser, P. M. (1994). Mangabey (*Cercocebus albigena*) population density, group size, and ranging: A twenty-year comparison. *Amer. J. Primatol.* 32: 197–205.

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

Peres, C. A. (1991). Humboldt's woolly monkeys decimated by hunting in Amazonia. *Oryx* 25: 89–95.

Poulsen, J. R., Clark, C. J., and Smith, T. B. (2001). Seasonal variation in the feeding ecology of the grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. *Am. J. Primatol.* 54: 91–105.

Quris, R. (1975). Ecologie et organization sociale de *Cercocebus galeritus agilis* dans le nord-est du Gabon. *La Terre et la Vie* 29: 337–398.

Range, F., and Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Tai National Park. *Am. J. Primatol.* 56: 137–153.

Rodgers, W. A., and Homewood, K. M. (1982). Biological values and conservation prospects for the forests and primate populations of the Udzungwa Mountains, Tanzania. *Biol. Conserv.* 24: 285–304.

Rogers, M. E., Abernethy, K. A., Fontaine, B., Wickings, E. J., White, L. J. T., and Tutin, C. E. G. (1996). Ten days in the life of a mandrill horde in the Lope Reserve, Gabon. *Am. J. Primatol.* 40: 297–313.

Rylands, A. B., and Keuroghlian, A. (1988). Primate populations in continuous forest and forest fragments in central Amazonia. *Acta Amazonica* 18: 291–307.

Schwartzkopf, L., and Rylands, A. B. (1989). Primate species richness in relation to habitat structure in Amazonian rainforest fragments. *Biol. Conserv.* 48: 1–12.

Shaw, N. F. (2003). *Foraging Strategies in Two Sympatric Mangabey Species (Cercocebus agilis and Lophocebus albigena).* Ph.D. Dissertation, Stony Brook University, Stony Brook, NY.

Skorupa, J. P. (1986). Responses of rainforest primates to selective logging in Kibale Forest Uganda: A summary report. In Benirschcke, K. (ed.), *Primates: The Road to Self-Sustaining Populations*, Springer, Berlin, pp. 57–70.

Stevenson, P. R. (2001). The relationship between fruit production and primate abundance in Neotropical communities. *Biol. J. Linnean Soc.* 72: 161–178.

Struhsaker, T. T. (1997). *Ecology of an African Rain Forest*, University Press of Florida, Gainesville, FL.

Struhsaker, T. T. (2002). *Guidelines for Biological Monitoring and Research in Africa's Rain Forest Protected Areas.* Unpublished Report, Center for Applied Biodiversity Science, Conservation International.

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

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

Thomas, S. C. (1991). Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. *Biotropica* 23: 68–83.

Tutin, C. E. G. (1999). Fragmented living: Behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. *Primates* 40: 249–265.

Tutin, C. E. G., Ham, R. M., White, L. J., and Harrison, M. J. S. (1997a). The primate community of the Lopé Reserve, Gabon: Diets, responses to fruit scarcity and effects on biomass. *Am. J. Primatol.* 42: 1–24.

Tutin, C. E. G., White, L. J. T., Mackanga-Missandzou, A. (1997b). The use by rain forest mammals of natural forest fragments in an equatorial African savanna. *Conserv. Biol.* 11: 1190–1203.

Wallis, S. J. (1978). *The Sociology of Cercocebus albigena johnstoni (Lyddeker): An Arboreal, Rain Forest Monkey*. Ph.D. Dissertation, University of London, London.

Waser, P. M. (1974). *Intergroup Interaction in a Forest Monkey: The Mangabey Cercocebus albigena*. Ph.D. Dissertation, Rockefeller University, New York, NY.
Waser, P. M. (1975). Monthly variation in feeding and activity patterns of the mangabey, *Cercocebus albigena* (Lyddeker). *East. Afr. Wildlife J.* 13: 249–263.
Waser, P. M. (1977). Feeding, ranging and group size in the mangabey *Cercocebus albigena*. In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys and Apes*, Academic Press, New York, NY, pp. 183–221.
Wasser, S. K. (1993). The socioecology of interspecific associations among the monkeys of the Mwanihana rain forest, Tanzania: A biogeographic perspective. In Lovett, J. C., and Wasser, S. K. (eds.), *Biogeography and Ecology of the Rain Forests of Eastern Africa*, Cambridge University Press, Cambridge, pp. 267–279.
Weisenseel, K., Chapman, C. A., and Chapman, L. J. (1993). Nocturnal primates of the Kibale Forest: Effects of selective logging on prosimian densities. *Primates* 34: 445–450.
Wieczkowski, J. A. (2003). *Aspects of the Ecological Flexibility of the Tana Mangabey (Cercocebus galeritus) in its Fragmented Habitat, Tana River, Kenya*. Ph.D. Dissertation, University of Georgia, Athens, GA.
Wilkie, D. S., and Flinn, J. T. (1990). Slash-burn cultivation and mammal abundance in the Ituri Forest, Zaire. *Biotropica* 22: 90–99.
Wilson, C. C., and Johns, A. D. (1982). Diversity and abundance of selected animal species in undisturbed forest, selectively logged forest and plantations in East Kalimantan, Indonesia. *Biol. Consen.* 24: 205–218.