




Cercopithecine and Colobine Abundance Across Protected and Unprotected Land in the Greater Mahale Ecosystem, Western Tanzania

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Abstract

Most primates live in unprotected land where abundances and threats may differ from those in protected areas. We therefore need to establish population densities in both unprotected and protected areas to effectively inform conservation planning. The Greater Mahale Ecosystem in western Tanzania is a region of mixed protected status with seven cercopithecine and colobine species: blue (*Cercopithecus mitis doggetti*), red-tailed (*C. ascanius schmidi*), and vervet (*Chlorocebus pygerythrus*) monkeys; ashy red colobus (*Piliocolobus tephrosceles*); black-and-white colobus (*Colobus angolensis*); and olive (*Papio anubis*) and yellow (*P. cynocephalus*) baboons. These species may be threatened by increasing human activity; however, except for ashy red colobus, no data on local abundances are available. We walked over 350 km of line transects in legally protected (Village Forest Reserves) and unprotected general land between August 2011 and October 2012 to estimate densities of primates and human activity. Primate densities were consistently low across the Greater Mahale Ecosystem. Blue and red-tailed monkey and ashy red colobus densities were especially low compared to populations in predominantly forested landscapes. Primate and human activity densities did not differ significantly inside and outside of reserves. Low primate densities could be natural responses to the lower proportions and quality of riparian forest habitat in the region. High levels of human activity and the absence of significantly higher primate densities in reserves suggest unprotected land could provide important refuges for primates in the Greater Mahale Ecosystem. This result further reinforces a broad need to include unprotected areas in primate conservation strategies.

Keywords Human disturbance · Mosaic landscape · Primate conservation · Village Forest Reserve

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Introduction

Primates are threatened across their range (Estrada *et al.* 2017), with species loss driven by direct (e.g., hunting and live capture) and indirect (e.g., habitat degradation and disease mortality) threats (Gillespie and Chapman 2008; Plumptre and Johns 2001; Wich and Marshall 2016). Monitoring primate abundance provides information on changes in population size and distribution and is essential for establishing whether a population is vulnerable to extinction (Campbell *et al.* 2016; Lawton 1993; Pearce and Ferrier 2001). Measuring population densities is therefore a necessary first step in establishing a plan to mitigate threats and subsequently assessing success of conservation action (Anderson *et al.* 2007; Chapman and Lambert 2000).

The types and magnitudes of threats faced by primates in unprotected landscapes can differ from those in protected areas (Tranquilli *et al.* 2014). Most data on primate abundance come from protected areas, however, which are often selected for surveying owing to high primate densities or the presence of charismatic taxa (e.g., great apes; Chapman and Peres 2001; Tranquilli *et al.* 2014). Assessing only a subset of a species' distribution may overestimate the importance of protected areas and underrepresent the role of unprotected areas that host large, often unmonitored populations. This risk is especially pertinent for relatively uncharismatic animals or species that live naturally at low densities (Cronon 1996; Gardner *et al.* 2007). Many studies also report intersite variation in human activities and interspecific variation in primate responses to threats (Estrada *et al.* 2017; Marsh and Chapman 2013). As such, conclusions from a single species or geographic area are not always applicable to other taxa or regions (Almeida-Rocha *et al.* 2017). To account for spatial heterogeneity of primate abundance and threats, data collected from landscape-scale surveys and protected area-level gradients should better reflect species distribution and conservation status (Arroyo-Rodriguez and Fahrig 2014; Caro 1999; Cavada *et al.* 2016).

The Greater Mahale Ecosystem (Fig. 1) in western Tanzania is a landscape in which there is a paucity of data on regional variation in primate abundance and local threats (Caro *et al.* 2009; Piel and Stewart 2014). Seven cercopithecine and colobine species occur in the Greater Mahale Ecosystem: Doggett's blue or silver monkey (hereafter, blue monkey; *Cercopithecus mitis doggetti*), red-tailed (*C. ascanius schmidti*) and vervet monkeys (*Chlorocebus pygerythrus*), ashy red colobus (*Piliocolobus tephrosceles*), black-and-white colobus (*C. angolensis*), and olive (*Papio anubis*) and yellow baboons (*P. cynocephalus*; see Methods). Chimpanzees (*Pan troglodytes schweinfurthii*) are also distributed throughout the region (Piel and Stewart 2014). Unlike relatively homogeneous, primarily forested environments, vegetation in the Greater Mahale Ecosystem is a mosaic of savanna-woodland with minimal riparian forest cover (Piel *et al.* 2015a). Data from the Issa Valley—the only long-term research site in the Greater Mahale Ecosystem outside of Mahale Mountains National Park—indicate that typically forest-dwelling species, such as *C. ascanius*, live at extremely low densities in these mosaics compared to forested sites (e.g., 4 individuals/km²; *cf.* 127 individuals/km² at Kibale, Uganda, Table I; Tapper *et al.* 2019; see also Piel *et al.* 2015a). However, except for an assessment of ashy red colobus in the southern half of the Greater Mahale Ecosystem (Moyer *et al.* 2006), there are no previous region-wide assessments of cercopithecine or colobine species abundance in the Greater Mahale Ecosystem and so the effect of vegetation cover on population density is not fully

understood. More broadly, all species listed here are classified as Least Concern on the IUCN Red List, except for ashy red colobus (Table 1). Lower densities in response to environment heterogeneity should increase local extinction risk for these species, especially in unprotected areas (Purvis *et al.* 2000). It is therefore unknown if these labels accurately reflect vulnerability in the Greater Mahale Ecosystem.

Human population growth in the Greater Mahale Ecosystem is extremely high (e.g., 4.2% annual increase from 2002 to 2012; *cf.* 2.7% for Tanzania overall, Tanzania National Bureau of Statistics 2012). This trend is due partly to Mishamo refugee settlement, which was established in 1972 and consisted of one settlement of >45,000 people at the time of study (Piel *et al.* 2015a; Fig. 1). With increased human activity in the region, high rates of poaching and habitat loss are the main threats to primates (Moyer *et al.* 2006). The only national park in the Greater Mahale Ecosystem—Mahale Mountains National Park—is at risk of isolation from surrounding forest due to increasing agriculture and road construction around park borders (Itoh *et al.* 2011; Piel and Stewart 2014). Outside of Mahale, protected land consists of Village Forest Reserves, in which conservation is partially decentralized from national government and managed by local communities (e.g., villages; Wily 2001; Wily and Dewees 2001). While protected areas should preserve higher animal densities relative to partially or unprotected areas (Caro 1999; Stoner *et al.* 2007), previous assessments of the effectiveness of Village Forest Reserves in conserving wildlife are mixed

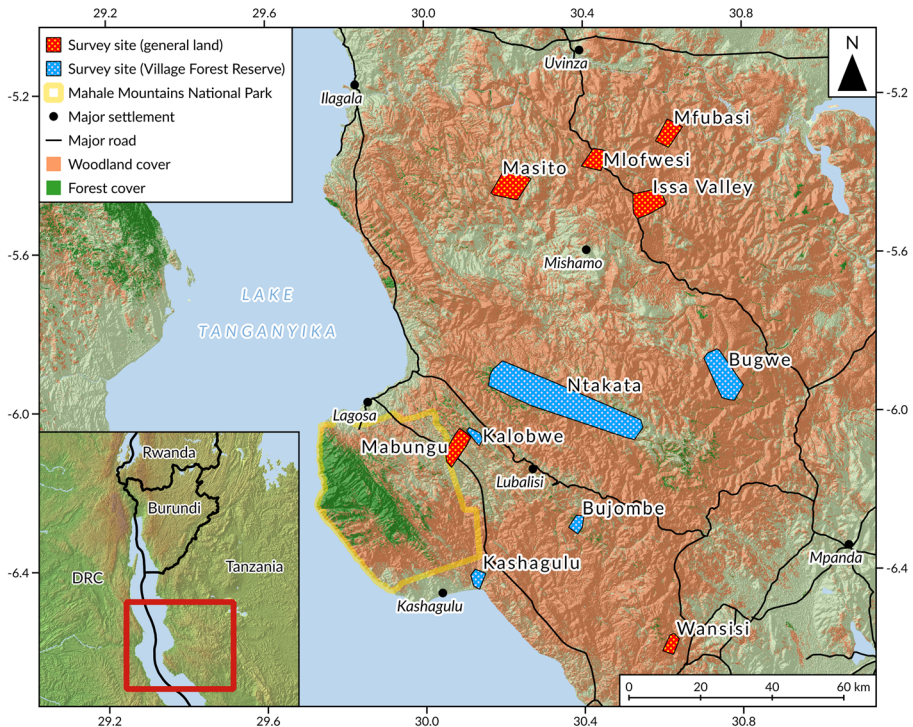


Fig. 1 Map of the Greater Mahale Ecosystem in western Tanzania. Minimum convex polygons surrounding all transects at each site are shown relative to the boundary of Mahale Mountains National Park and major settlements and roads in the region.

Table 1 IUCN Red List statuses and densities from other East African sites for the cercopithecin and colobine species investigated in this study

Species	IUCN Red List status (reference)	Country	Site	Density [range] (individuals/km ²)	Density [range] (groups/km ²)	Reference
Blue monkey (<i>Cercopithecus mitis</i>)	Least Concern (Kingdon <i>et al.</i> 2008c)	Democratic Republic of Congo	Ituri	24.2 ± 7.5SE		Thomas (1991)
		Kenya	Kakamega (Isecheno)	220.0	5.0	Fashing and Cords (2000)
		Tanzania	Mahale Mountains NP	4.0	0.4	Uehara (2003)
		Uganda	Budongo Forest Reserve	15.6–58.2		Plumptre and Reynolds (1994)
			Kibale NP (Kanyawara)		1.0	Chapman <i>et al.</i> (2000)
			Ituri		18.9 ± 4.4SE	
Red-tailed monkey (<i>C. ascanius</i>)	Least Concern (Oates <i>et al.</i> 2008)	Democratic Republic of Congo	Lomako	42.8		McGraw (1994)
		Kenya	Kakamega (Buyangu)	176.0		Gathua (2000)
		Tanzania	Kakamega (Isecheno)	72.0		Cords (1984)
			Issa Valley	0.68–4.0	0.11–1.28	Tapper <i>et al.</i> (2019)
		Uganda	Mahale Mountains NP	115.5	7.7	Uehara (2003)
			Budongo Forest Reserve	8.3–46.4		Plumptre and Reynolds (1994)
Ashy red colobus (<i>Ptilocolobus tephrosceles</i>)	Endangered (Struhsaker 2016)	Uganda	Kibale NP (Kanyawara)	70.0–175.0		Struhsaker (1980); Struhsaker (1997)
		Tanzania	Kibale NP (Ngogo)	131.5		Struhsaker and Leland (1988)
			Mahale Mountains NP	105.0	3.5	Uehara (2003)
			Ulupi (Mbizi)	0.02	1.0	Davenport <i>et al.</i> (2007)
			Ulupi (Mbuzi)	0.05	1.5	Davenport <i>et al.</i> (2007)
			Kibale NP (Kanyawara)	295.8		Struhsaker (1980)
Olive baboon (<i>Papio anubis</i>)	Least Concern (Kingdon <i>et al.</i>)	Uganda		Mean 4.7 [3.2–6.1]		Chapman and Chapman (1999)
		Kenya	Kibale NP (multiple sites)	0.6	5.5	Chapman <i>et al.</i> (2000)
			Loita Hills		0.01	Butynski and de Jong (2012)
				0.11	de Jong and Butynski (2010)	

Table 1 (continued)

Species	IUCN Red List status (reference)	Country	Site	Density [range] (individuals/km ²)	Density [range] (groups/km ²)	Reference
	2008a)		Mathews Range Forest Reserve			
Yellow baboon (<i>P. cynocephalus</i>)	Least Concern (Kingdon <i>et al.</i> 2016)	Uganda	Budongo Forest Reserve	11.0–14.0		Plumptre and Reynolds (1994)
		Kenya	Amboseli NP	1.2 ^a		Samuels and Altmann (1991)
		Tanzania	Mahale Mountains NP	80.0	1.6	Uehara (2003)
Vervet monkey (<i>Chlorocebus pygerythrus</i>)	Least Concern (Kingdon <i>et al.</i> 2008b)	Kenya	Amboseli NP	Mean 233.0 [126.6–321.2]		Struhsaker (1967)
			Amboseli NP	Mean 25.7		Lee and Hauser (1998)
			Loita Hills		0.01	Butynski and de Jong (2012)
			Mathews Range Forest Reserve		0.02	de Jong and Butynski (2010)

Densities refer to undisturbed habitat, where specified. NP = national park; SE = standard error.

^a >95% of study population consisted of yellow baboons.

(reviewed in Brockington 2007; Ribot *et al.* 2010). Moreover, to our knowledge no study has yet quantitatively assessed primate abundance inside and outside of Village Forest Reserves (see Roe *et al.* 2009).

We surveyed 11 geographically independent sites in the Greater Mahale Ecosystem in 2011–2012 to estimate densities of cercopithecine and colobine species and human threats. We tested two hypotheses that could explain these densities. First, we hypothesized that densities are influenced by habitat quality, primarily by vegetation cover. Given a lack of prior data on almost all of our study species in forest-scarce mosaic habitat, we predicted that all primates across the region show lower densities than in more forested sites elsewhere. Second, we hypothesized that protected areas harbor greater primate densities than unprotected areas, in part due to reduced human threats. As such, we predicted Village Forest Reserves show higher primate densities and lower threat densities than unprotected, general land does.

Methods

Study Area and Survey Sites

The Greater Mahale Ecosystem is a *ca.* 18,200 km² area bordered by the Malagarasi River to the north, the Ugalla River to the east, the southern border of Mahale Mountains National Park to the south, and Lake Tanganyika to the west (Fig. 1). Land cover is a mosaic of primarily miombo woodland, thin patches of riparian forest, larger patches of evergreen forest, and tracts of open grassland and seasonal swamps (Moyer *et al.* 2006). We collected data on monkey abundance during a landscape scale survey of chimpanzee habitat. We surveyed 10 different survey sites based on results from Conservation Action Planning workshops held during 2008–2010 that identified key areas for chimpanzee habitat (Piel and Stewart 2014; see Electronic Supplementary Material [ESM] Table SI for detailed descriptions). We conducted surveys from August 2011 to September 2012, and we also included data collected from January 2011 to December 2012 by the Greater Mahale Ecosystem Research and Conservation Project at the Issa Valley.

Sites were either Village Forest Reserves or general land with no formal protected status at the time of the surveys. Village Forest Reserves in the Greater Mahale Ecosystem are one designation of land under community-determined Village Land Use Plans, alongside zones set aside for residential buildings, agriculture, woodlots, etc. (Jane Goodall Institute 2009). This decentralization of conservation management aims to reduce conflict between communities and potentially distant national government (Wily and Dewees 2001). Specifically, these reserves are designed to allow forests to recover from overexploitation while encouraging shifts to sustainable resource extraction and livelihoods (e.g., ecotourism). As such, human activity in Village Forest Reserves is prohibited without village council permission, and several villages employ forest scouts or village forest monitors to actively police their reserves (Piel and Stewart 2014).

Data Collection and Study Species

At each site, two observers walked transects (range: 4–23 transects per site) of at least 1.2 km in length (\bar{x} : 4.3 km; maximum: 7.3 km; see ESM Table SI). At each site, we

positioned an initial transect at the center of the area of interest, following a randomly selected 30 degrees bearing. We then positioned subsequent transects parallel to the initial transect at *ca.* 800-m intervals across the survey site. Observers walked each transect once at a pace of 1 km/h. At the Issa Valley, we walked a minimum of three (\bar{x} : 6) of seven parallel transects distributed across the site at 0.3–1.2 km intervals every month except December 2011 as part of long-term data collection. On all transects, where we encountered obstacles (e.g., cliffs), we recorded the positions where we abandoned and resumed the transect and used the shortened length in analyses. AP and FS collected almost all data, trained field assistants at the Issa Valley in the protocol, and tested interobserver reliability to confirm that we did not need to control for observer variability in our analyses.

For each observation of primates or illegal human activity, we recorded perpendicular distance (from the transect to the center of the primate group or activity), group size, and vegetation class (see later). We measured perpendicular distances of <10 m using a measuring tape and >10 m using a Nikon Laser Rangefinder 550AS. We defined a primate group as multiple individuals of the same species in clearly observable close proximity, as per Buckland *et al.* (2010). We categorized vegetation classes as closed canopy riparian forest ($\geq 50\%$ connected canopy), open canopy riparian forest (<50% connected canopy), woodland, grassland, swamp, or converted land (road or cropland). We classified observations of human activity as one of three threat types reflecting increasing magnitudes of threat to primates: disturbance, hunting, or permanent land conversion (see ESM S1 for definitions; ESM Table SIII).

We collected data on all cercopithecine and colobine species in the Greater Mahale Ecosystem except for black-and-white colobus, which are restricted to high-altitude forest in Mahale Mountains National Park (Moyer *et al.* 2006). In relation to baboons, *Papio anubis* are found only in the far north of the Greater Mahale Ecosystem, with most observations of phenotypically *anubis*-like animals in the Greater Mahale Ecosystem likely to be *P. cynocephalus* \times *P. anubis* hybrids. Phenotypically *P. kindae*-like baboons are found in Mahale Mountains National Park (Zinner *et al.* 2015) and as far north as the Issa Valley (AP *unpubl. data*; C. Jolly *pers. comm.*), although taxonomy remains unresolved in these areas (as per Zinner *et al.* 2015). Because we could not always reliably differentiate between *P. cynocephalus*, *P. kindae*, and hybrids, we grouped observations of any of these animals as “baboons.”

Line Transect Analyses

Observation distances differed between vegetation classes because of variation in visibility. We recategorized vegetation classes into two habitat types: open habitat (open canopy riparian forest, woodland, grassland, swamp, and converted land) or closed habitat (closed canopy riparian forest). We used Distance 7.0 (Thomas *et al.* 2010) to calculate effective strip widths (ESW) separately for open and closed habitat across all sites combined by stratifying by habitat type.

We measured the length of each transect walked in open and closed habitat using AWiFS satellite imagery (see ESM S1 for details). We calculated densities by dividing the number of observations by area of open or closed habitat surveyed (area = length \times 2ESW) at each site. To control for the high variation in closed habitat cover between sites, we calculated densities using only the area for the habitat type occupied primarily (>75% observations in a single habitat type) by each species in the Greater Mahale

Ecosystem (as per Caro 2001): closed habitat for red-tailed monkey, blue monkey, and ashy red colobus; open habitat for baboons and vervet monkey. We calculated single densities of each human activity for open and closed habitat combined. We condensed some observations of human activity because we could not always reliably count individual instances within a particular activity (e.g., we grouped any number of cattle in a herd as a single observation; see ESM Table SII).

Statistical Analyses

We used Mann-Whitney-Wilcoxon tests in R 3.5.1 (R Core Team 2018) to compare primate and human activity densities between Village Forest Reserves and unprotected sites ($N = 5$ Village Forest Reserves; $N = 6$ unprotected sites; ESM Table SI). Given the low number of observations of any primate species, to provide a sufficient sample size we pooled densities for each of open and closed habitat species across all transects for each site. We excluded a single outlying value for closed habitat species at Bugwe. We tested for collinearity between primate density and proportion of forest cover across all sites because we expected Village Forest Reserves to be implemented in areas of higher forest cover than general land. There was no significant difference in forest cover in Village Forest Reserves compared to general land (Mann-Whitney U test: $N = 11$ sites, $U = 6.000$, $P = 0.126$). Forest cover was correlated with closed habitat species density (Kendall tau-b correlation: $\tau = 0.601$, $P = 0.012$) and open habitat species density ($\tau = -0.554$, $P = 0.032$). We therefore weighted densities by proportions of open and closed habitat cover at each site for open and closed habitat species, respectively.

Ethical Note

We collected data with permission from the Tanzania Wildlife Research Institute (TAWIRI), the Tanzanian Commission for Science and Technology (COSTECH), and Kigoma and Mpanda district governments; and in accordance with all applicable guidelines for the observation of wild animals in Tanzania. The authors declare that they have no conflict of interest.

Data Availability The data analyzed in this study are available from the corresponding author on reasonable request.

Results

We observed each of our study species on at least one occasion (Table II). Except for blue monkeys, which we observed at only one site (Ntakata), we observed each species at a minimum of two survey sites (maximum: six sites for ashy red colobus). There was no site with observations of all five species (maximum: four species at the Issa Valley), and at two sites (Kashagulu and Masito) we did not observe any species. The highest densities we observed were shown by red colobus at Bujombe (67.1 individuals and 4.3 groups/km²; Table II) and Bugwe (outlying values: 209.1 individuals and 26.1 groups/km²). Vervet monkeys and baboons showed the lowest maximum densities across all sites (0.2

and 7.5 individuals/km² at Mabungu and Bugwe, respectively), followed by blue monkeys (10.4 individuals/km² at Ntakata) and red-tailed monkeys (32.3 individuals/km² at the Issa Valley). Densities (individuals/km²) were substantially lower for each species than those reported at other sites (Table I). Neither densities for closed habitat nor open habitat species pooled (individuals/km²) differed significantly between Village Forest Reserves or general land sites (Mann-Whitney-Wilcoxon tests: $N = 11$ sites; open habitat species: $Z = 0.995$, $P = 0.320$; closed habitat species: $Z = -0.910$, $P = 0.363$).

We observed human activity at all 11 sites (Table III). The most widespread threat we observed was evidence of habitat disturbance, which was found at all but one site (Kalobwe). Similarly, evidence of land conversion was observed at all but two sites (Issa and Kashagulu). Evidence of hunting was the least frequently encountered threat. We observed evidence of hunting at only 6 of 11 sites, and densities were also substantially lower than the other threat types (Fig. 2). Similar to primate densities, densities of either threat type (observations/km²) did not differ significantly with protected status (Mann-Whitney-Wilcoxon tests: $N = 11$ sites; disturbance: $Z = 1.095$, $P = 0.273$; hunting: $Z = 1.869$, $P = 0.062$; land conversion: $Z = 1.095$, $P = 0.273$).

Discussion

We found cercopithecine and colobine densities across the Greater Mahale Ecosystem to be lower across both protected and unprotected areas compared with numbers reported from tropical forests, in line with our first prediction. Our findings corroborate previous studies from the Issa Valley that found forest-dwelling primate species living at lower densities compared to forest-dominated landscapes (e.g., Piel *et al.* 2015a). This is likely due mostly to the low proportion of riparian forest cover in savanna-woodland mosaics, which results in a wider distribution of resources for forest primates compared to predominantly forested environments (Isbell and Young 1996). Consequently, lower food availability may constrain densities of these species (Hemingway and Bynum 2005; Piel *et al.* 2017). For example, similar low densities reported for red-tailed monkeys at the Issa Valley and chimpanzees in the Greater Mahale Ecosystem are associated with large home ranges that are required to meet daily nutritional requirements from patchily distributed food (Ogawa *et al.* 2007; Tapper *et al.* 2019).

Interspecific competition and predation pressure also influence population densities (Chapman *et al.* 2004). For example, monkeys compete with chimpanzees for woodland and riparian forest foods at the Issa Valley (Piel *et al.* 2017). In addition, chimpanzees are known to prey upon red-tailed, blue, and red colobus monkeys at primarily forested sites, e.g., Gombe, Tanzania (Wrangham and van Zinnicq Bergmann Riss 1990) and Kibale, Uganda (Watts and Mitani 2002). While increased chimpanzee abundance could be expected to constrain monkey densities, chimpanzee densities reported by at each site broadly reflect the densities we observed for monkeys (Piel and Stewart 2014). Specifically, Ntakata, Kalobwe, and Bujombe—the three sites with the highest proportions of riparian forest—had the highest chimpanzee densities and comprised three of the four sites from this study with the highest densities of closed habitat species overall. Interspecific differences in abundance may therefore relate more strongly to the extent of suitable habitat for these primates in the Greater Mahale Ecosystem. Primate communities typically show high species nestedness as suitable habitat increases in area (Irwin 2016). For forest

Table II Densities of primate species at 11 survey sites across the Greater Mahale Ecosystem estimated from January 2011 to January 2012

Survey site	Survey effort (km ²) [95% CI]			Density (individuals/km ²) [95% CI]					Density (groups/km ²) [95% CI]				
	Closed habitat	Open habitat		Blue monkey	Red-tailed monkey	Ashy red colobus	Baboons	Vervet monkey	Blue monkey	Red-tailed monkey	Ashy red colobus	Baboons	Vervet monkey
Bugwe	0.08 [0.06–0.10]	5.18 [4.61–5.83]				209.1 [165.2–264.5]	7.5 [6.7–8.5]				26.1 [20.7–33.1]	0.8 [0.7–0.9]	
Bujombe	0.46 [0.37–0.58]	1.77 [1.57–1.99]			67.1 [53.0–84.9]						4.3 [3.4–5.5]		
Issa Valley	2.44 [1.93–3.09]	102.70 [91.28–115.53]			32.3 [25.5–40.9]	0.8 [0.6–1.0]	6.2 [5.5–7.0]			4.5 [3.6–5.7]	0.4 [0.3–0.5]	0.5 [0.4–0.5]	
Kalobwe	0.24 [0.19–0.31]	1.15 [1.02–1.29]			28.9 [22.9–36.6]	8.3 [6.5–10.5]				8.3 [6.5–10.5]	8.3 [6.5–10.5]		
Kashagulu	0.10 [0.08–0.13]	1.84 [1.64–2.07]					0.7 [0.6–0.8]	0.2 [0.2–0.2]				0.2 [0.2–0.2]	0.2 [0.2–0.2]
Mabungu	0.40 [0.32–0.51]	5.91 [5.25–6.65]											
Masito	0.13 [0.10–0.16]	5.36 [4.76–6.03]											
Mfibusi	0.05 [0.04–0.06]	5.03 [4.47–5.65]					1.4 [1.2–1.6]					0.2 [0.2–0.2]	
Mlofvesi	0.02 [0.02–0.03]	4.56 [4.05–5.13]					1.1 [1.0–1.2]					0.4 [0.4–0.5]	
Niakata	1.54 [1.22–1.95]	6.62 [5.93–7.50]		10.4 [8.2–13.1]	13.9 [11.0–17.6]	37.3 [29.5–47.2]			3.2 [2.6–4.1]	3.2 [2.6–4.1]	6.5 [5.1–8.2]		
Wansisi	0.40 [0.32–0.51]	2.22 [1.98–2.51]				32.5 [25.7–41.1]				0.0 [0.0–0.0]	2.5 [2.0–3.2]		

Empty cells indicate absence of any observations. CI = confidence interval.

primates, this effect may constrain densities in a heterogeneous, mosaic environment where suitable habitat should be smaller in area, more patchily distributed, and offer lower quality food compared to forests (Piel *et al.* 2017; Tapper *et al.* 2019).

Densities (individuals/km²) for baboons and vervet monkeys were also low compared to other sites outside of the Greater Mahale Ecosystem (Table I). A lack of resources is less likely to explain these differences given that vegetation in the Greater Mahale Ecosystem is much more typical for these species than for forest monkeys. Although disturbance could explain low densities, both baboons and vervet monkeys are known to be highly adaptable to human presence (Hill 2000). While we did not observe high rates of hunting in the Greater Mahale Ecosystem, given that hunting is pervasive in other areas of western and southwestern Tanzania (e.g., Davenport *et al.* 2007; Mgawe *et al.* 2012), the complete absence of these animals at many sites could indicate previous extirpation or shifts to hunting tactics that leave fewer evidence behind (e.g., with guns; *cf.* snares, Piel *et al.* 2015b).

Low densities suggest that forest-dwelling monkeys are likely more vulnerable to human threats than in areas supporting higher densities (Purvis *et al.* 2000). Specifically, we found evidence of a decline in abundance for ashy red colobus—the most endangered species we investigated and the only species for which a previous density in the Greater Mahale Ecosystem is available. Moyer *et al.* (2006) calculated a mean density of 74.6 individuals/km² for ashy red colobus from surveys conducted in 2005 across Ntakata, Wansisi, and additional sites south and southwest of Mishamo (Fig. 1); over double our average of 32.3 individuals/km². This decline could be due to poor behavioral flexibility in the face of increased human pressure. Forest-adapted primates like colobus monkeys that have much larger home ranges in savanna-mosaics may be especially vulnerable to habitat degradation and should therefore be slow to shift ranges to undisturbed areas (Irwin 2016) or recover if degradation stops (Chapman *et al.* 2000; Isaac and Cowlshaw 2004). Moreover, vegetation type influences species susceptibility to threats. In forests, primates are particularly vulnerable to land conversion that reduces tree cover, while in woodlands and grasslands, primates are more easily hunted or ensnared (Isaac and Cowlshaw 2004; Kümpel *et al.* 2008). In heterogeneous environments, primates that utilize multiple vegetation types, e.g., red-tailed monkeys (McLester *et al.* 2018; Tapper *et al.* 2019), should therefore encounter a greater diversity of threats, which may exacerbate population decline.

We observed higher rates of indirect threats (e.g., disturbance) than direct threats (e.g., hunting and land conversion). All of our study species show some resilience to habitat disturbance. For example, olive baboons in Kenya preferentially follow roads (Strandburg-Peshkin *et al.* 2017) and vervet monkeys in Uganda forage on crops with relatively low rates of retaliatory killing by farmers (Saj *et al.* 2001). Resilience may also delay short-term declines in forest primate densities (red-tailed monkeys, red colobus: Struhsaker 1997; blue monkeys: Mammides *et al.* 2009) or lead to temporarily increased densities (e.g., *Colobus guereza*: Fashing 2002; *C. angolensis palliatus*: Marshall *et al.* 2005). These trends may be partly due to preference by these species for food in secondary vegetation that results from logging (Mammides *et al.* 2009; Thomas 1991). Nonetheless, red colobus and red-tailed and blue monkeys show wide intraspecific variation in these responses (e.g., Chapman *et al.* 2000; Plumptre and Reynolds 1994), possibly as the result of habitat-specific dietary flexibility (Nowak and Lee 2013). Furthermore, even though primates in the Greater Mahale Ecosystem that

Table III Densities of human activities across the Greater Mahale Ecosystem estimated from January 2011 to January 2012

Survey site	Survey effort (km ²) [95% CI]			Density (observations/km ²) [95% CI]				
	Closed habitat	Open habitat		Disturbance	Hunting	Land conversion	Total	
Bugwe	0.04 [0.02–0.06]	1.04 [0.93–1.17]		29.6 [25.9–33.6]		1.8 [1.6–2.1]	31.4 [27.5–35.7]	
Bujombe	0.23 [0.15–0.37]	0.36 [0.32–0.40]		13.5 [10.3–17.3]	5.1 [3.9–6.5]	32.2 [24.5–41.0]	50.8 [38.7–64.8]	
Issa Valley	1.24 [0.78–1.98]	20.68 [18.38–23.28]		0.2 [0.2–0.3]	0.2 [0.2–0.3]	0.1 [0.0–0.1]	0.5 [0.4–0.6]	
Kalobwe	0.12 [0.08–0.20]	0.23 [0.20–0.26]				5.7 [4.4–7.1]	5.7 [4.4–7.1]	
Kashagulu	0.05 [0.03–0.08]	0.37 [0.33–0.42]		2.4 [2.0–2.8]			2.4 [2.0–2.8]	
Mabungu	0.20 [0.13–0.33]	1.19 [1.06–1.34]		16.5 [13.8–19.4]	5.0 [4.2–5.9]	9.3 [7.8–11.0]	30.8 [25.8–36.3]	
Masito	0.06 [0.04–0.10]	1.08 [0.96–1.21]		6.1 [5.3–7.0]	0.9 [0.8–1.0]	4.4 [3.8–5.0]	11.4 [9.9–13.0]	
Mfubasi	0.02 [0.01–0.04]	1.01 [0.90–1.14]		50.2 [44.2–56.9]	5.8 [5.1–6.6]	32.8 [28.9–37.2]	88.8 [78.2–100.7]	
Mlofwesi	0.01 [0.01–0.02]	0.92 [0.82–1.03]		46.3 [40.9–52.3]	3.2 [2.9–3.6]	10.8 [9.5–12.2]	60.2 [53.3–68.1]	
Niakata	0.78 [0.49–1.25]	1.34 [1.19–1.51]		6.1 [4.7–7.7]		0.9 [0.7–1.2]	7.1 [5.4–8.9]	
Wansisi	0.20 [0.13–0.32]	0.45 [0.40–0.50]		10.7 [8.4–13.3]	1.5 [1.2–1.9]	20.0 [15.7–24.7]	32.2 [25.3–40.0]	

Empty cells indicate absence of any observations. CI = confidence interval.

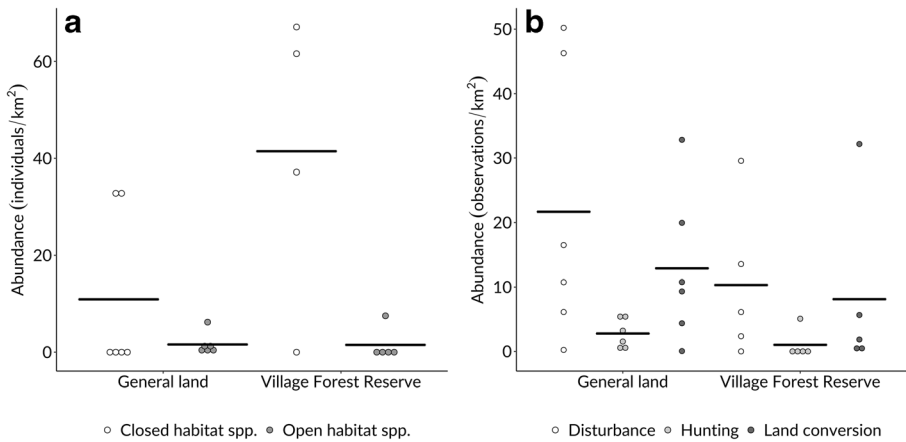


Fig. 2 Variation in densities of open and closed habitat species (**a**) and human activities (**b**) between general land and Village Forest Reserves across the Greater Mahale Ecosystem estimated from January 2011 to January 2012. Black horizontal lines indicate mean values.

exploit both forest and woodland foods (e.g., Tapper *et al.* 2019) could therefore be expected to tolerate disturbed habitat for longer than forest populations, previous studies have demonstrated disproportionate increases in habitat degradation following even low levels of initial disturbance (the “Pandora’s Box Effect”: Laurance *et al.* 2009). Resilience to human activity is therefore unlikely to lead to long-term population survival in the Greater Mahale Ecosystem, particularly if rates and intensities of habitat degradation will only increase over time (Nowak and Lee 2013).

We did not find formal protection to result in significantly higher primate densities, in contrast to our prediction. Forest primate densities are expected to be low in mosaic environments, which complicates conservation strategies. Specifically, discerning whether these species are well adapted and naturally surviving at low densities, or instead experiencing population decline and therefore severely at risk, will require rigorous and standardized long-term monitoring (Chapman *et al.* 2000). In the Greater Mahale Ecosystem, the need for continuous monitoring is particularly high because of the infrequency of surveys thus far. For example, the densities we report in this study are at least 7 yr old, and given high rates of habitat degradation and human encroachment in the region, these numbers may overestimate actual species abundances at the time of publication.

The absence of many species in both protected and unprotected areas may also explain a lack of significant difference without indicating an ineffectiveness of Village Forest Reserves. Specifically, absences may reflect the challenges of surveying monkeys that require direct observations to be identified (e.g., in contrast to chimpanzees, which are identifiable from nests or relatively conspicuous scat). For example, red-tailed and blue monkeys typically produce only sporadic vocalizations (e.g., male “pyows” and “pops”) or hide in silence in response to potential predators passing below (Detwiler 2010). Substantial variation in forest monkey group size and spread between savanna-woodland mosaics and forests may also influence observation rates in these environments (as per Plumpton 2000; e.g., see McLester *et al.* 2019). Moreover, transects were designed with the primary aim of investigating evidence of chimpanzee presence in both open and closed vegetation. While forest monkeys do use open vegetation in the Greater Mahale Ecosystem, they typically remain close to forest

edges and retreat into forest in response to humans or predators. As such, even though we controlled for forest proportions when calculating densities, time spent in large tracts of open vegetation likely reduced opportunities for observing forest monkeys. Future surveys should repeat transect walks, particularly in forest patches, to maximize search effort (e.g., as recommended by Teelen 2007), while analyses should control for habitat-specific patterns of group size and spread, where known.

Village Forest Reserve status did not have a significant effect in deterring human encroachment. Instead, we found the lowest levels of human activity at the Issa Valley. Given the permanent research station at this site, this result further suggests that researcher presence can deter habitat encroachment (Campbell *et al.* 2011; Laurance 2013; Piel *et al.* 2015b). The Issa Valley is the closest buffer to expansion of Mishamo and a continued researcher presence will likely be integral to future conservation in this area. Nonetheless, researcher presence alone is unlikely to replace large-scale protected areas and if well funded and actively enforced, protected areas remain important strategies in conserving wildlife (Tranquilli *et al.* 2014).

Strengthening enforcement of existing Village Forest Reserves and implementing new reserves in the Greater Mahale Ecosystem were priorities for recent Conservation Action Planning workshops (TANAPA 2015). More data on Village Forest Reserve management, ideally obtained directly from local communities, are needed to recommend appropriate improvements for current Village Forest Reserves in the Greater Mahale Ecosystem. Similarly, locations and types of reserves are best determined by benefits that should be identified for local communities as well as wildlife (Geldmann *et al.* 2013; Salerno *et al.* 2015). Devolving conservation management to the village level through Village Forest Reserves remains a relatively recent (1998) concept in Tanzania (e.g., compared to the national park system; Wily and Dewees 2001). Given previously identified risks of Village Forest Reserve mismanagement (e.g., increased corruption; Brockington 2007), these reserves require careful administration in their infancy if they are to provide long-term benefits to people and wildlife alike. In the meantime, unprotected land that remains undisturbed seems likely to become increasingly important refuges for primates in the Greater Mahale Ecosystem if human encroachment into primate habitat continues to increase. As such, our results provide a starting point from which long-term trends in primate abundance and human activity in the Greater Mahale Ecosystem can be established and furthermore reinforce the need for continuous monitoring both inside and outside of protected areas to inform the most effective conservation strategies for primate populations in this region.

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Author Contributions AP and FS conceived the study and developed methodology. AP, FS, and LP collected data. EM analyzed the data and wrote the manuscript; other authors provided editorial advice.

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