


Long-term dynamics of wild primate populations across forests with contrasting protection in Tanzania

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Abstract

Anthropogenic activities driving tropical forests' loss imperil global biodiversity and provision of ecosystem services. In this context, systematic monitoring programs evaluating wildlife trends are essential. Non-human primates are relevant conservation targets since they represent vital components of tropical forests by serving as pollinators and seed dispersers. Here, we present primate group counts data collected over 19 years in a primate hotspot in Tanzania. We analyzed data with a hierarchical dynamic model accounting for imperfect detection that estimates local group abundance and temporal rates of change, to assess whether habitat protection explained trends of the arboreal and diurnal Peters' Angola colobus (*Colobus angolensis palliatus*), Udzungwa red colobus (*Piliocolobus gordonorum*), and Tanzania Sykes' monkey (*Cercopithecus mitis subsp. moloneyi*). We targeted populations occurring in two forest blocks with contrasting protection regimes, with one block impacted by targeted poaching of the two *Colobus* species. We found that these latter species were much less abundant in the more human impacted forest, underwent a rapid decline, and subsequently remained at low abundance and without signs of recovery once this forest was granted greater protection. Instead, Sykes' abundance did not differ between forests, and improved protection was associated with a slight increase in abundance. Age class composition for social groups of both *Colobus* species differed between forests, indicating altered births and survivorship rates in the impacted forest. Results suggest that targeted hunting can prevent recovery for several years and even after increased habitat protection. Our approach appears valuable to monitor population dynamics over the long term, highlighting species-specific variations in both vulnerability to anthropogenic disturbance and recovery patterns in primate populations.

KEYWORDS

demography, N-mixture models, primate abundance, primate conservation, primate decline, primate monitoring, Udzungwa

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1 | INTRODUCTION

Tropical forests, 18% of which are found in Africa, are of global importance for biodiversity conservation and provision of ecosystem services (Berti & Svenning, 2020; Brockerhoff et al., 2017; Steur et al., 2020). Their current, unparalleled loss imperils global biodiversity more than any other contemporary phenomenon, jeopardizing the global provision of these services, and therefore affecting humans' well-being (Butchart et al., 2010; Cardinale et al., 2012; Hooper et al., 2005; Terraube & Fernández-Llamazares, 2020). Under the pledge to meet global targets (e.g., Aichi Biodiversity Targets and Sustainable Development Goals) to avert this crisis, systematic monitoring programs evaluating wildlife conservation status over time remain the key tool to understand processes that operate over long temporal scales (Collen et al., 2008; Haase et al., 2018; Havstad & Herrick, 2003; Likens & Lindenmayer, 2018). In this context, mammalian populations are of exceptional relevance given their critical role in promoting forest regeneration (Gardner et al., 2019; Luskin et al., 2019). Specifically, by serving as important pollinators and seed dispersal over long distances, non-human primates (primates hereafter) represent essential components of tropical biodiversity (Chapman et al., 2013, 2020; Heymann, 2011). However, unsustainable human activities affecting habitat loss (i.e., intensive agriculture, logging, livestock farming, construction of new road networks, as well as oil and gas drilling) and poaching/illegal trade have driven 76% of primate population to decline, and 60% are threatened with extinction (de Almeida-Rocha et al., 2017; Estrada et al., 2017; Marsh et al., 2013). Besides such threats that directly impact primate abundance and demography (Barelli, Mundry, et al., 2015; Rovero et al., 2012), also human pressure and habitat integrity play a major role on host health by altering gastrointestinal microorganisms (Barelli, Albanese, et al., 2015, 2020, 2021).

In this context, monitoring primate populations in tropical forests affected by human impact is critical, and an effective approach is to contrast populations from areas with similar ecological characteristics but different protection levels and anthropogenic disturbance (e.g., Chapman et al., 2010; McLester et al., 2019; Oberosler et al., 2020; Rovero et al., 2012). However, primate monitoring programs that span over a sufficient period to enable evaluation of temporal trends, and potential recovery following conservation interventions, are surprisingly few (e.g., Chapman et al., 2000, 2018). Factors that can prevent success of these programs include the difficulties in ensuring continuous and consistent data collection in the long-term due to lack of funding, diversification in the use of protocols and inter-observer variability, all of which may lead to data biases or data gaps (e.g., Rovero et al., 2015); moreover, primates are long-lived animals with a slow life history, and hence, recovery may, at best, be detected several years after perturbation or improved conservation (Strier & Ives, 2012). However, studies on other long-lived vertebrates, such as snapping turtles (*Chelydra serpentina*), show limited evidence of population recovery after 23 years from a major decline (Keevil et al., 2018). This implies that species with slow life history are more sensitive to adult survivorship (Jonsson

& Ebenman, 2001) and take longer to recover from depletion. Thus, they are extremely vulnerable to density-dependent factors, and greater effort should be allocated to monitoring them.

Here, we use data collected over 19 years to assess temporal dynamics of three common arboreal and diurnal primate species in the Udzungwa Mountains in Tanzania. For each species, we targeted populations occurring in two distinct areas that underwent contrasting management regimes in the past decades, and whereby recent increased protection has been allocated to the previously poorly protected area (details in *Study areas*). The Udzungwa Mountains has a long history of primate research. Of relevance here, long-term primate monitoring was established in the more protected forest in 2002 (Rovero et al., 2006) and replicated in the unprotected forest since 2004 (Rovero et al., 2012). Previous trend analyses showed a marked and rapid decline of primate populations in the poorly protected forest while relative stability was detected in the well-protected forest (Rovero et al., 2015). While the decline was detected for all three species (two species of colobine monkeys and one *Cercopithecus* monkey), it resulted especially dramatic for the colobine monkeys as they are targeted by selective hunting (Rovero et al., 2012). In 2017, however, the poorly protected forest was upgraded from Forest Reserve to Nature Reserve, which represents a higher protection status. This came with the allocation of more staff and resources for managing the forest and thanks to the support of conservation agencies a program of monthly anti-poaching patrols begun (Southern Tanzania Elephant Program, 2021).

Given this background, we markedly extended the sampling period relative to Rovero et al. (2015) to estimate temporal trends in local abundance (i.e., group counts). We analyzed primate counts using *N*-mixture models (Dail & Madsen, 2011) that allowed us to account for imperfect detection of animals. We extended the analytical procedures by including the size of primate groups as a detection covariate given the finding that group size affects detectability of target species (Cavada et al., 2016). We also extended the previous dataset by collecting data on age categories of individuals living in the primate groups to evaluate differences in group size and composition between areas. Thus, we aimed to determine (a) whether trends continued to differ between the two areas or signs of population recovery appear in the area where protection has increased, and (b) whether group size and composition differed between areas. We predicted that temporal trends are species-specific and that only the *Cercopithecus* monkey shows signs of recovery given its lower vulnerability to hunting (Cronin et al., 2016). However, we also expected that all primate species would show signs of variation in group size (i.e., small group size, lower natality, and survivorship) in the poorly protected forest where the abundance of feeding trees is expected to be lower (Mbora et al., 2009; Struhsaker, 2010) compared to the better protected one where food availability is greater. Moreover, in forests where hunting pressure is highest, we expected group composition (in terms of age classes) not to be influenced as much as in species with faster life histories, where younger age classes are disproportionately impacted by showing more variation in population growth rate (Bjørkvoll et al., 2012; Jonsson & Ebenman, 2001; Sæther et al., 2005).

2 | METHODS

2.1 | Ethics statement

The authors confirm they did not interact with or disrupt any of the primate species surveyed in any way. Data collection used distance sightings of animals, with no direct contact or interaction with the animals. Highly trained fieldworkers strictly adhered to the “Code of Best Practices for Field Primatology” published by the International Primatological Society (IPS) as well as the “Principles for the Ethical Treatment of Primates” of the American Society of Primatologists (ASP). Data collection complied with legal requirements and laws governing wildlife research in Tanzania. Research permits to FR were obtained through the Tanzania Commission for Science and Technology (COSTECH), Tanzania Wildlife Research Institute (TAWIRI), Tanzania National Parks (TANAPA), and Tanzania Forest Services Agency (TFS).

2.2 | Study area and animal populations

The study area is located within the Udzungwa Mountains (7° 40' S–8° 40' S and 35° 10' E–36° 50' E; [Figure 1](#)) in the southern-most range of the Eastern Arc Mountains which belong to Eastern Afromontane biodiversity hotspot (<https://www.cepf.net/our-work/biodiversity-hotspots/eastern-afromontane>) and extends over 19,000km² (Platts et al., 2011). Rainfall averages 1500–2000mm per year concentrated in two periods: November–December and March–May. Elevation across the Udzungwa Mountains spans between 270 and 2576 m a.s.l., while in the targeted forests it ranges from 290 to 2250 in Mwanihana (MW) and from 270 to 2100 in Udzungwa Scarp (US). The forest cover forms a mosaic of moist forest blocks, interspersed with a matrix of naturally drier habitats, but also croplands and settlements. In the past 50–60 years, these forested areas have been gradually separated into several forest blocks by both natural events (i.e., geology and climate) and human activities (i.e., subsistence and commercial logging, pole cutting agriculture, bushfires: Ruiz-Lopez et al., 2016). Some of these forest blocks differ in habitat structure, vegetation parameters and have different protection level (from good protection in National Parks, to poorer protection in other types of reserves) affecting primate populations living around the protected areas (Barelli, Mundry, et al., 2015; Cavada et al., 2019; Ruiz-Lopez et al., 2016). However, the two forest blocks under study are markedly similar in terms of ecological characteristics but have contrasting protection regimes. These forests are as follows: (1) MW, a protected forest located within the boundaries of the Udzungwa Mountains National Park; and (2) US, a Nature Reserve designated as such in 2017 from a poorly protected Forest Reserve (Rovero & Barelli, 2017), located 150 km to the southwest of Mwanihana. For decades, by lacking effective law enforcement on the ground, US has suffered from uncontrolled hunting of colobus monkeys and habitat degradation, leading primates to a marked decline (Rovero et al., 2015). Besides the similar elevation gradient, both forests are covered by a similar gradient of vegetation types,

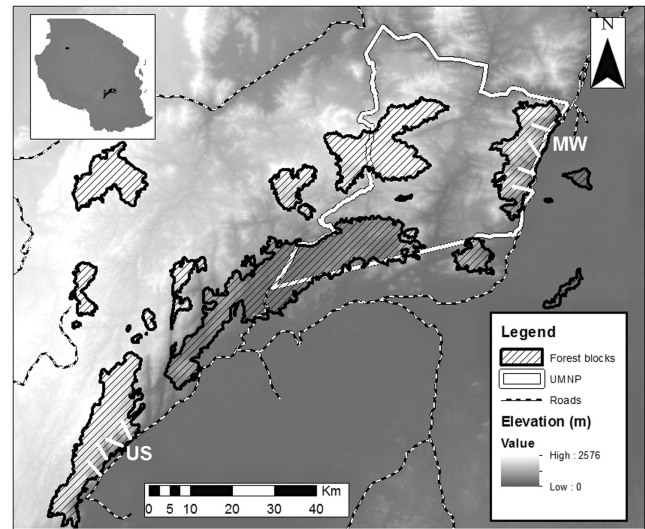


FIGURE 1 Map of the Udzungwa Mountains of Tanzania (location in the top left inset). The map shows the forest blocks among which are Mwanihana forest (MW) to the northeast and Udzungwa Scarp (US) to the southwest. The four line transects used to count primates are shown as white lines in each of these two forests. The background layer is a Digital Elevation Model (dark is lower elevation). The borders of the Udzungwa Mountains National Park (UMNP) are also indicated. Reproduced from Rovero et al. (2015).

from deciduous, lowland forest to evergreen, montane, and upper montane forest (Rovero et al., 2015). Importantly moreover, previous research has indicated that the structure and diversity of canopy trees along the sampled transects do not differ significantly between forests (Rovero et al., 2012); predation pressure on primates can be assumed higher in MW, as leopards (*Panthera pardus*) are considered extirpated from US, and there are no reasons to assume different densities of crowned eagles (*Stephanoaetus coronatus*), the main aerial predator of primates, between these forests.

Among the diurnal non-human primates present in the two areas, this study will consider three species:

- Udzungwa red colobus (*Piliocolobus gordonorum*) which are endemic primates of the Udzungwa Mountains and have been recently upgraded as vulnerable by the IUCN Red List but live in fragile and highly fragmented landscapes (IUCN 2021). These monkeys live in large social groups (up to 60 individuals) and are primarily arboreal and folivorous;
- Peters' Angola colobus (*Colobus angolensis palliatus*) has experienced reduction in abundance at heavily disturbed sites (Rovero et al., 2012). Similar to Udzungwa red colobus, Peters' Angola colobus are present in both forests but appear to be relatively more common at higher elevations (Marshall et al., 2005). They generally form groups comprising one-male and multiple females ranging in size from 2 to at least 14 individuals. Similarly, to the pattern observed for Udzungwa red colobus, group size decreases in degraded forests (Marshall et al., 2005). They are typically arboreal and feed predominantly on mature leaves;

c. Tanzania Sykes' monkey (*Cercopithecus mitis spp. moloneyi*) prefers secondary, regenerating and semi-deciduous forest zones (Rovero et al., 2006). Differently from the two colobines, Sykes' monkey is an opportunistic species that uses all vertical forest strata and feeds predominantly on fruits. They also live in one-male/multi-female groups, ranging in size from 2 to at least 22 individuals (Rovero et al., 2006), and they are associated with both Udzungwa red colobus and Peters' Angola colobus.

(small to large) were identified as either individuals clinging on their mothers (small infants), those of approximately 25% of adult size (medium infants), or 25–33% of adult size (large infants); juveniles (small to large) were identified as independent individuals of clearly smaller size than adults (33–80% adult size), while adults were mature individuals, a category which (in our case) included subadults (Struhsaker, 2010). All observers were trained in data collection procedures by FR, who was also the only non-local observer involved in the field.

2.3 | Data collection

Primate surveys were conducted during the dry months (from June to November) from 2002 to 2020 (with a gap in part of 2005 for MW and in 2006 for both forests; Table 1) along four line transects in each forest. Sampling in the dry season was logistically easier than in the wet season, yet an earlier analysis did not find significant differences in estimated local abundance and detectability between seasons (Rovero et al., 2015). Regularly maintained trails were used as transects which were predominantly oriented east to west, between 3.5 and 4 km in length, and located from forest edge to interior, that is, sampling the lower to mid-elevation forest zones in both forests (300 to 1000 m a.s.l.). Transects were walked at least once per month by two observers, one responsible for data recording (main observer) and one assisting. Over the 19 years of data collection, 5 observers were involved overall, resulting in 7 different combinations of pairs, with no significant differences in detectability (Rovero et al., 2015). A smaller number of transect walks was achieved in US forest, compared to MW, due to its remoteness and also because one transect (Jkt) was discontinued in 2007 as it fell within a military zone, and replaced with a new one (Tazara) established in 2009. Primate surveys began in the morning at 7–7:30, and observers walked at a pace of 1 km per hour. When primate groups were spotted, the main observer annotated time, position along transect, and primate species detected. Despite the difficulties of counting individuals in the densely vegetated habitat, we also recorded the (minimum) number of individuals in each group sighted. Through additional focal training to observers, during 2016–2020 we also collected data on group composition in terms of age categories: infants, juveniles, and adults. Infants

2.4 | Statistical analysis

We used 19 years of data to analyze spatio-temporal patterns in primate abundance of three species, within two forests with a different level of protection. We based our model formulation on a prior version developed by Rovero et al. (2015) that investigated seasonal and annual group variations of primate abundance by adopting an exponential growth model, which is a hierarchical generalization of a *N*-mixture model (Dail & Madsen, 2011; Royle, 2004). We modified the model by including group size as detection covariate. This has already proven to be critical to avoid underestimation of animal densities and abundances, particularly for species with small social units that can go easily undetected (Cavada et al., 2016, 2017). Thus, we modeled the observed group counts of each primate species (y_{itk}), during the *k*th visit to the *i*th site (transect in our case) in year *t*, as the result of two processes: the state (ecological process) describing the true local abundance (N_{it}), and the observation process that links y_{itk} to N_{it} . We assumed:

$$N_{i1} \sim \text{Poisson}(\lambda),$$

with λ being the average expected group abundance among all transects of the two areas (MW and US) for the first year ($t = 1$);

$$N_{it} \sim \text{Poisson}(\gamma_{\text{area}} N_{it-1}),$$

with γ_{area} being the area-specific finite rate of population increase, for other years ($t = 2-19$);

$$y_{ijt} \sim \text{Binomial}(N_{it}, p_{itk}),$$

| Forest | Transect | Length (km) | Sampling year | Census replicates |
|--------|-------------|-------------|----------------------|-------------------|
| MW | Camp site 3 | 4.0 | 2002–2004, 2007–2020 | 179 |
| | Msolwa | 4.0 | 2007–2020 | 152 |
| | Mwanihana | 4.0 | 2002–2004, 2007–2020 | 179 |
| | Sanje | 3.7 | 2002–2004, 2007–2020 | 177 |
| US | Ikule | 3.6 | 2004–2005, 2007–2020 | 89 |
| | Jkt | 3.7 | 2004–2005, 2007 | 14 |
| | Mkaraji | 3.5 | 2004–2005, 2007–2020 | 87 |
| | Tazara | 3.6 | 2009–2020 | 69 |

TABLE 1 Survey information for line transects in the protected (Mwanihana, MW) and unprotected (Uzungwa Scarp, US) forest in the Udzungwa Mountains of Tanzania, sampled for primate group counts in the dry season (June–November) during 2002–2020.

with p_{itk} being the detection probability during the visit k (1- K) to transect i (1- R) in year t (1- T). We assumed the detection probability of each species may differ among transects and may be influenced by animal group size as follows:

$$\text{logit}(p_{itk}) = \mu_p + \alpha_{\text{gsize}} * \text{gsize}_{i,t,k} + \varepsilon_i$$

with $\varepsilon_i \sim \text{Normal}(0, \sigma_{\text{transect}}^2)$ and “gsize” being the standardized average group size of the primate species along each transect i during the k th visit in year t . To properly account for uncertainty about missing group-size values due to missing surveys, we specified an underlying model for the covariate, by assigning a prior distribution as follows:

$$\text{gsize}_{i,t,k} \sim \text{Normal}(\pi_{\text{gsize}})$$

where π_{gsize} is the probability vector associated with each group-size value that we assume is drawn from a uniform distribution between 0 and 1. We estimated area-specific group abundance for year t as: $N_{\text{area},t} = \sum_{i=R_{\text{area},\text{min}}}^{i=R_{\text{area},\text{max}}} N_{it}$ with $R_{\text{area},\text{min}} = 1$ for MW and 5 for US, and $R_{\text{area},\text{max}} = 4$ for MW and 8 for US. We compared group abundances among the two areas by dividing the annual area-specific abundances by the total length of the transect (TLT , in km) in each area, as

$$\frac{N_{\text{area},t}}{\sum_{i=R_{\text{area},\text{min}}}^{i=R_{\text{area},\text{max}}} TLT_i}$$

We implemented the models in a Bayesian framework using JAGS (Plummer, 2003) via R (version 3.6.3; R Core Team, 2021) with the jagsUI (version 1.5.1; Kellner, 2019) package. We generated three parallel chains of 70,000 iterations with an adaptation of 1000, a burn-in of 5000 iterations and thinning by 20 for a total of 9750 draws that were used to derive summaries of parameter posterior distribution. We specified Uniform(0,20) prior distribution for λ , Uniform(-5,5) prior distribution for γ_{area} , Uniform(0,2) for $\sigma_{\text{transect}}^2$, and a Normal(0,0.01) distribution for μ_p . Convergence of the Markov chains was satisfactory based on the Gelman-Rubin statistic (Gelman & Rubin, 1992). The model code is reported in Appendix S1, and data for the analysis are available at the link <https://figshare.com/articles/dataset/>.

We also used the group composition data for 2016–2020 to derive average observed group size and composition in the three age categories and lumping all years, given the limited sample size that prevented inter-annual comparisons. We assessed differences in group size and composition between forests using Wilcoxon Signed Rank tests.

3 | RESULTS

3.1 | Group dynamics

A total of 946 census walks were conducted along eight transects (four in each area; Table 1). Individual transects were surveyed for 3–17 years (median 16). Group counts per individual transect census

walk ranged from 0 to 6 for all species, with mean values of encounter rate (groups/km) being 0.123 and 0.009 for red colobus in MW and US, respectively, 0.095 and 0.004 for Peters' Angolan colobus, and 0.072 and 0.122 for Tanzania Sykes' monkey (Figure 2a,c,e). Estimated group abundance from modeling was higher in MW than US for both colobus monkeys, whereas it was relatively similar for Tanzania Sykes' monkey (Figure 2b,d,f). We estimated trend coefficients for population abundance to be on average close to zero for the protected forest of MW ($\gamma_{\text{MW}} = -0.01$, 95% $BCI: -0.10 - 0.08$ for Peters' Angola colobus; -0.01 , $-0.10 - 0.08$ for Udzungwa red colobus; 0.01 , $-0.10 - 0.11$ for Tanzania Sykes' monkey; Table 2, Figure 2). We found instead a decreasing trend for the unprotected forest of US for both Peters' Angola colobus ($\gamma_{\text{US}} = -0.32$, $-0.68 - -0.03$) and Udzungwa red colobus (-0.25 , $-0.53 - -0.01$), while we found population stability for Tanzania Sykes' monkey (0.02 , $-0.11 - 0.14$). Mean detection probability p ranged from 0.15 (0.05–0.29) for Peters' Angola colobus to 0.27 (0.18–0.37) for Tanzania Sykes' monkey (Table 2). Transect-specific variability in detection σ_{transect} ranged from 0.36 (0.02–1.01) for Tanzania Sykes' monkey to 0.90 (0.20–1.81) for Udzungwa red colobus. Further, we found detection probability of all the three species to be positively influenced by group size ($\alpha_{\text{gsize}} = 0.32$, 0.21–0.42 for Peters' Angola colobus; 0.18, 0.08–0.30 for Udzungwa red colobus; 0.36, 0.25–0.46 for Tanzania Sykes' monkey; Figure 3).

3.2 | Demography

During 2016–2020, we recorded only three encounters of Peters' Angola colobus in US, with an average of 3.67 adults per group and neither group had any juveniles nor infants. In MW, the 551 groups sighted had an average of 3.99 adults, 0.12 juveniles and 0.21 infants (Figure 4). Udzungwa red colobus groups in MW had an average total group size of 20.67 individuals, with 14.52 adults, 2.86 juveniles and 3.28 infants ($N = 868$), which was higher than in US where we recorded an average group size of 15.20, with 11.50 adults, 1.40 juveniles and 3.28 infants, respectively ($N = 10$). The differences were significant for the total group size ($W = 6180$, $p < .05$) and for juveniles ($W = 6541$, $p < .005$), and marginally non-significant for adults ($W = 5869.5$, $p = .053$) and infants ($W = 5747.5$, $p = .066$). In contrast, Tanzania Sykes' monkeys had a significantly smaller average group size in MW (3.71, $N = 577$) than in US (4.18, $N = 346$; $W = 86,779$, $p < .001$); adults were also fewer in MW (3.55, $N = 577$) than US (3.97, $N = 346$; $W = 86,090$, $p < .001$), while the differences in juveniles (0.11 and 0.13 for MW and US) and infants (0.05 and 0.08) had the same directionality but were not significant ($W = 98,473$, $p = .43$ and $W = 97,877$, $p = .14$ for juveniles and infants, respectively).

4 | DISCUSSION

We used primate monitoring data collected over a span of 19 years, analyzed with a hierarchical dynamic model that accounts for

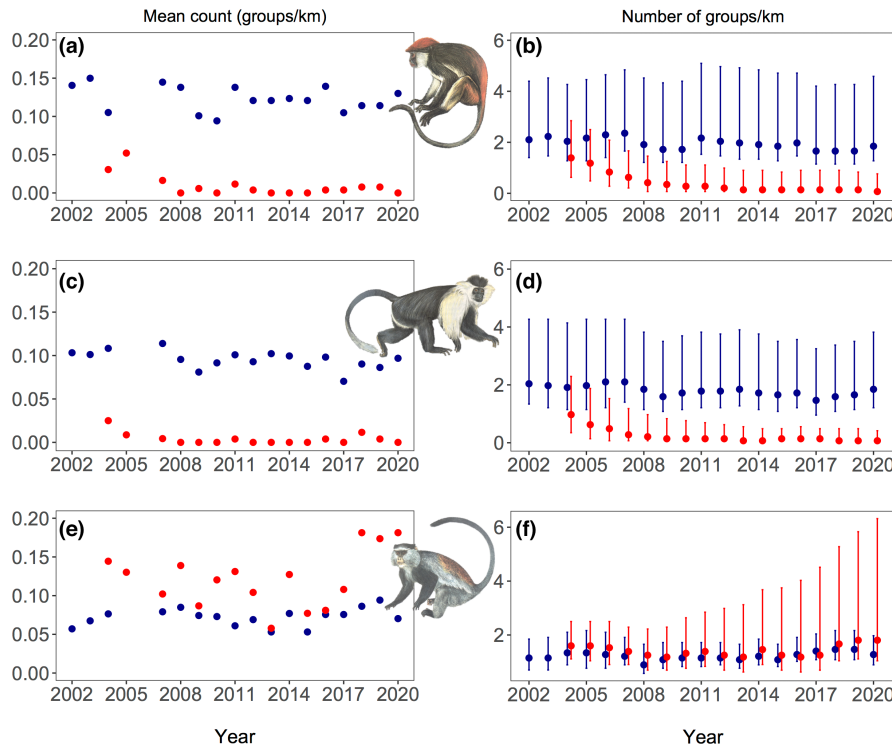


FIGURE 2 Mean observed counts (group/ km) in the forest of Mwanihana (blue circles) and Uzungwa Scarp (red circles) in Tanzania for Udzungwa red colobus (a), Peters' Angola colobus (c) and Tanzania Sykes' monkey (e), while (b), (d), and (f) show the estimated total number of groups per km (posterior median and 95% BCI) for the corresponding species and forest.

TABLE 2 Summaries of posterior distributions of model parameters for count data of three primate species (Peters' Angola colobus, Udzungwa red colobus, and Tanzania Sykes' monkey) for a protected (Mwanihana, MW) and a non-protected (Uzungwa Scarp, US) forest in the Udzungwa Mountains of Tanzania.

| Parameter | Peters' Angola colobus (<i>Colobus angolensis</i>) | Udzungwa red colobus (<i>Ptilocolobus gordonorum</i>) | Tanzania Sykes' monkey (<i>Cercopithecus mitis monoides</i>) |
|----------------------------|--|---|--|
| | Mean (95% BCI) | Mean (95% BCI) | Mean (95% BCI) |
| λ | 8.64 (4.44–16.81) | 9.05 (4.87–17.26) | 5.14 (2.73–8.41) |
| γ_{MW} | -0.01 (-0.10–0.08) | -0.01 (-0.10–0.08) | 0.01 (-0.10–0.11) |
| γ_{US} | -0.32 (-0.68 to -0.03) | -0.25 (-0.53 to -0.01) | -0.02 (-0.11–0.14) |
| p | 0.15 (0.05–0.29) | 0.18 (0.06–0.33) | 0.27 (0.18–0.37) |
| σ_{transect} | 0.83 (0.08–1.83) | 0.90 (0.20–1.81) | 0.36 (0.02–1.01) |
| α_{gsize} | 0.31 (0.21–0.42) | 0.18 (0.08–0.30) | 0.36 (0.25–0.46) |

Note: λ is average expected abundance (during the first year) among all transects of the two areas; γ_{MW} and γ_{US} are the changing rates for the independent population of groups at each area; p is mean detection probability in probability scale (i.e., $p = \text{expit}(\mu_p)$); σ_{transect} is the standard deviation for the unexplained variability among transects; α_{gsize} is the effect of group size on detection probability.

imperfect detection to estimate local abundance, to infer whether differences in anthropogenic disturbance as previously assessed (Barelli, Mundry, et al., 2015; Cavada et al., 2019) and upgraded level of habitat protection over time may explain temporal variations in primate group abundance. Although we cannot exclude that other factors such as feeding tree diversity, predation pressure or natural diseases may contribute to differences that we found between forests in temporal trends and abundance of primates, the known ecological features seem unlikely to account for such differences (see Methods). For example, predation pressure can rather be assumed higher in MW than US, and the available data on vegetation structure and diversity along transects are also not consistent with the decline and lower abundance of colobines in US

than MW (Rovero et al., 2012). Although we lack longitudinal data on how these ecological factors may have varied over the sampling period, no major environmental event was observed besides the upgraded protection status of US, where before 2017 protection efforts in terms of ground patrols were virtually absent. Since the Nature Reserve was established, protection efforts increased but have remained largely uneven between the two areas. Indeed, as of 2022 the Udzungwa Mountains National Park operates with 50 armed rangers and an annual budget for protection of approximately 130,000 USD (Abel Mtui, pers. comm.), while Uzungwa Scarp Nature Reserve operates overall with approximately 50,000 USD (Godfrey Nyangaresi, pers. comm.) and only two permanent staff dedicated to protection.

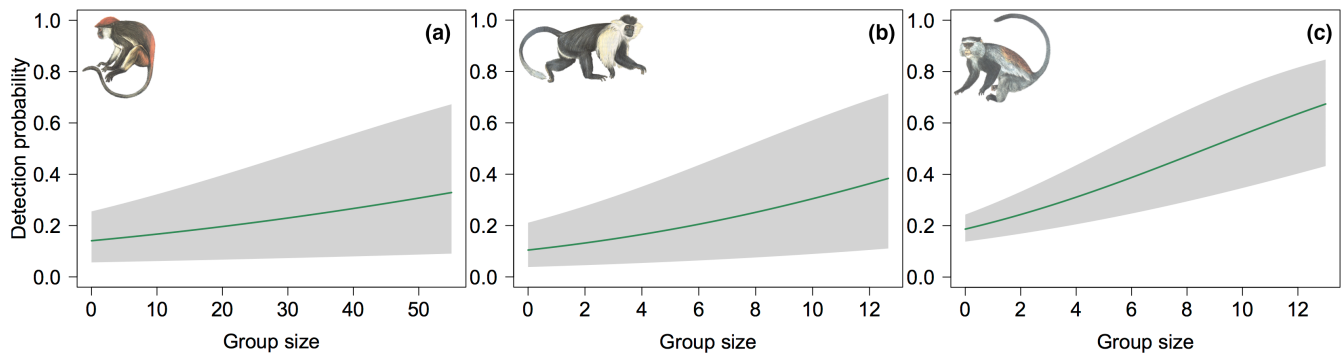


FIGURE 3 Effect of group size on detection probability for Udzungwa red colobus (a), Peters' Angola colobus (b), and Tanzania Sykes' monkey (c).

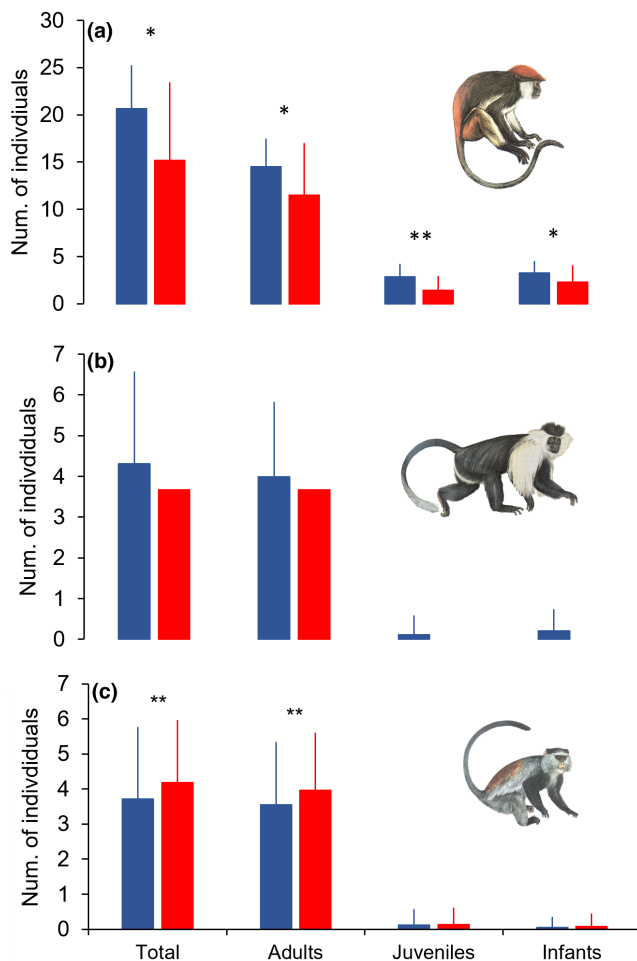


FIGURE 4 Mean (error bars represent SD) number of individuals of (a) Udzungwa red colobus, (b) Peters' Angola colobus, and (c) Tanzania Sykes' monkey for the total size and each of three age categories in the social units sighted during 2016–2020 in the Mwanihana forest (blue bars) and Uzungwa Scarp Nature Reserve (red bars) in Tanzania. Asterisks denote significance differences at $p < .01$ (two asterisks) and $p < .05$ (one asterisk).

These differences in protection effort are very relevant to our results that indicate that populations of the two colobine monkeys underwent a rapid decline during the first few years of data

collection in US, the southern, poorly protected forest, while population of Sykes' monkeys did not show signs of decline. These findings extend the results from a previous analysis based on a period that was 8-years shorter than the current one (Rovero et al., 2015). Our extended dataset allowed us to assess that following this decline populations remained apparently stable, albeit at very low levels of local abundance, with Tanzania Sykes' monkeys showing sign of recovery in the last 6 years, concomitant with the upgraded level of protection of the poorly protected forest and the initiation in 2017 of a protection program that implements monthly ground patrols lasting 4–5 days by a team of reserve rangers, village game scouts and armed soldiers from the regional anti-poaching unit (Southern Tanzania Elephant Program, 2021). While the target primate species are relatively long-lived (Jones, 2011) and hence a lag from the onset of protection to recovery is to be expected (Ewers & Didham, 2006; Nagelkerke et al., 2002), evidence from other studies shows that effective ground protection can be associated with relatively rapid population recovery (e.g., Chapman et al., 2018; kipunji, *Rungwecebus kipunji*: Davenport et al., 2022).

It is widely reported that illegal hunting can cause fast declines of primate populations (de Thoisy et al., 2005; Estrada et al., 2017; Oates, 1996), mirroring results from a preliminary assessment in the same study system indicating the overwhelming effect of hunting on habitat degradation in explaining the lower abundance and decline of colobine monkeys in the poorly protected compared to the well-protected forest (Rovero et al., 2012). Colobine monkeys move in the canopies as relatively large and well detectable social units, making themselves an easier target of hunters, that use rifles and dogs to isolate such groups in canopy trees (Rovero et al., 2012; Topp-Jørgensen et al., 2009). Instead, no significant difference in estimated group abundance was observed for the Tanzania Sykes' monkey over the years and between forests. In fact, a slightly higher local abundance was estimated in the poorly protected and degraded forest, suggesting that Tanzania Sykes' monkeys are less targeted by illegal hunting, likely due to their faster and more terrestrial locomotion pattern. However, it cannot be excluded that the degraded and regenerating habitat in US may be more optimal for Sykes' monkeys (Rovero et al., 2012) which has more flexible diet (i.e., frugivorous and folivorous) and has wider habitat preferences. These characteristics,

as observed in lemur species (Eppley et al., 2020), may make them less susceptible to habitat degradation than the colobines, which may explain their relatively higher abundance in the poorly protected forest (Cavada et al., 2019). Whether such species-specific variations between forests and along years are due to dietary habits or annual fruiting have not been investigated; however, results from other longitudinal studies addressing these questions are not so conclusive (Chapman et al., 2010). Likewise, additional studies will be required to assess whether the generalist Tanzania Sykes' monkeys are able to occupy ecological niches, previously occupied by the specialist primates, as suggested in theoretical studies (Ramadantsoa et al., 2018) and other model species (Matthew et al., 2014).

Besides extending considerably the monitoring period relative to earlier assessments, we included groups size in the *N*-mixture model as a covariate of detectability, which proved to be important as it was significantly associated with detectability for all three species, matching results in the same area from studies that used hierarchical distance sampling to estimate population abundance (Cavada et al., 2016).

Moreover, although data are partial and only available for a subset of years, data collected on group composition over the last five years of the monitoring program allowed us to assess variations in primate demography between forests. While we collected these data in view of the high experience of observers, we could rarely perform total counts during transect walk; hence, we acknowledge that these data are qualitative in nature and meant to provide preliminary insights into group composition patterns. Indeed, due to the inability of accurately identifying primate gender at every observation, we were unable to calculate standard survivorship (i.e., ratios of subadults and juveniles per adult female) and natality (i.e., ratios of infants per adult female) indices (e.g., Struhsaker, 2010). However, our findings revealed that group size in relation to age categories differs significantly across primate species and between forests. Although too few group sightings of Peters' Angola colobus living in the poorly protected forest were available to enabling us for statistical comparisons, the counts of individuals from those living in the well-protected forest show that groups of Peters' Angola colobus may face a strong challenge during both the juvenile and infant stage. Most of the individuals spotted were adults (93%, this category including subadults) while the remaining were juveniles (2%) and infants (4%) of any stage (large, middle, small), indicating that few infants were born in the last five years and/or most of them did not survive. Sample size for Udzungwa red colobus was large enough to draw more accurate conclusions and pinpoint significant differences between forest types, suggesting that hunting and human disturbance may influence not only colobines population abundance, but also their demographic parameters (Struhsaker, 2010). Udzungwa red colobus from the well-protected forest showed percentages of adults (70%), juveniles (14%) and infants (16%) in the range of those observed in previous ad libitum monitoring (between 1998 and 2000) from the same population (Mwanihana forest: Struhsaker et al., 2004), other forest patches in its proximity (Kalunga forest: Struhsaker et al., 2004), and different red colobus species from other countries (e.g., *P. temminckii* and *P. tephrosceles*: Struhsaker, 2010).

Indeed, Udzungwa red colobus living in the poorly protected forest showed higher percentage of adults (75%) and infants (21%) indicating a higher rate of natality, while a significant reduction of the juvenile category (9%) may indicate a much lower survivorship. Similar discrepancy between infants and juveniles' category was also reported in a highly fragmented forest from previous monitoring (Magombera forest: Struhsaker, 2010). Such low counts of juveniles can be attributed to several factors. For example, natural predation is one of the major forces potentially explaining it (Struhsaker, 2010; Watts & Mitani, 2002), but habitat disturbance and illegal hunting pressure, although reduced during the latest years, cannot be totally excluded. Moreover, stronger competition for food from other group members (Struhsaker et al., 2004) or unexpected outcomes from previous population compression (Struhsaker, 2010) should also be taken into account while interpreting the demographic variations found. Similar composition in age categories confirms that Tanzania Sykes' monkeys are not suffering of disturbance in the poorly protected forest as for the colobines, and the slightly larger group counts (average group size in US: 4.18 and MW: 3.71) are confirming their possible thriving in more degraded habitat.

In conclusion, our results from the long-term data collection in the Udzungwa forests suggest that prompt protection actions are needed for the conservation of primates. These should primarily translate into increased intensity and coverage of anti-poaching patrols, and secondarily continued ecological monitoring to assess management effectiveness, in addition to community education, engagement into protection and provision of alternative livelihoods. Following the assumption that protected forests receive less anthropogenic pressure (i.e., less illegal hunting and less habitat degradation), forests are expected to recover over time and likewise primate population abundance. Our finding that population abundance was not improving over time but remained under a certain threshold suggests that signs of recovery are possible, although highly dependent on species-specific vulnerability to habitat changes and biological adaptations.

AUTHOR CONTRIBUTION

FR and CB conceived the study. FR, ASM, and SS carried out data collection. VO and NC implemented the dataset and led the statistical analyses. CB and FR wrote the manuscript with assistance from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at <https://doi.org/10.6084/m9.figshare.22059383.v1>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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