



On the move: Activity budget and ranging ecology of endangered Ashy red colobus monkeys (*Piliocolobus tephrosceles*) in a savanna woodland habitat

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ARTICLE INFO

Keywords:

Red colobus
Activity patterns
Day range
Home range
Chala Forest
Ufipa Escarpment
Western Tanzania

ABSTRACT

The majority of primate species are under the threat of extinction and their numbers are decreasing worldwide mainly due to human activities. Most primates outside protected areas survive in habitats with different degrees of anthropogenic alterations. Thus, the persistence of a primate species across its geographic range partly depends on the ability of its populations to adapt to diverse habitats with different spatiotemporal patterns of food availability. Understanding the ecological and behavioral adaptations of a particular species to the different habitats it occupies is crucial for designing a comprehensive conservation approach that can also benefit sympatric wildlife species. Ashy red colobus (*Piliocolobus tephrosceles*) are arboreal, folivorous and endangered monkeys that occur in Uganda and Tanzania. They have been studied in forest habitats, but very little is known about their behavior and ecology in savanna woodland and how these arboreal and folivorous monkeys can survive in such dry habitats. To better understand this species' range of adaptations, from July 2016 to June 2018 we conducted a comparative study of habitat quality, activity budget and ranging ecology of two groups of Ashy red colobus monkeys living in distinct habitats in western Tanzania: savanna woodland and forest mosaic. We found that the savanna woodland group spent significantly more time moving and less time feeding than the forest mosaic group. We also found that the savanna woodland group had a larger home range, core areas and mean daily travel distance than the forest mosaic group. The savanna woodland group had the largest home range size ever reported for Ashy red colobus monkeys or other red colobus species. Seasonal differences in home range and core area size were found for

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<https://doi.org/10.1016/j.gecco.2023.e02440>

Received 22 September 2022; Received in revised form 20 February 2023; Accepted 17 March 2023

Available online 20 March 2023

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the forest mosaic group (both were larger in the dry than in the wet season) but not for the savanna woodland group. The patchy spatial distribution and lower density of most of the preferred food tree species of Ashy red colobus monkeys in the savanna woodland seemed to influence their ranging behavior in this habitat. These results expand our understanding of colobine behavioral and ecological flexibility and provide critical data to formulate workable conservation strategies that encompass the whole range of habitats occupied by Ashy red colobus monkeys. Our study also helps to better understand the ecological constraints that savanna woodland habitats pose on primates.

1. Introduction

Due to the escalation of anthropogenic activities, most primate species are threatened with extinction or declining in numbers, and forced to occupy human modified landscapes (Arroyo-Rodríguez et al., 2017; Estrada et al., 2012, 2017; Galán-Acedo et al., 2019; McLennan et al., 2017). The continued presence of a primate species across its geographic range depends, at least in part, on the ability of its populations to adapt to human-induced changes. To understand how primates can survive and adapt to such changes, it is necessary to conduct behavioral ecology studies in all types of habitats a species occupies (Chaves and Bicca-Marques, 2016). Such data on a species range of ecological and behavioral adaptations are essential for designing successful and comprehensive conservation strategies for that species (Wieczkowski, 2005; Yan et al., 2018). For example, determining intraspecific variation in home range size is vital in planning reserves for a species (Caro and Durant, 1995; Di Franco et al., 2018; Powell, 2000) and understanding its vulnerability to extinction (Davidson et al., 2009).

Red colobus monkeys (*Piliocolobus*) are highly threatened colobines (subfamily Colobinae), with more than three quarters of their taxa listed either as Critically Endangered or as Endangered according to the IUCN (International Union of Conservation of Nature) Red List (Struhsaker, 2010; Linder et al., 2021). They are specialized folivores, but include other types of foods in their diet such as seeds, fruit, bark and invertebrates (Chapman and Chapman, 1999; Struhsaker, 2010; Steel, 2012). They have a four-chambered stomach containing bacteria to help digest cellulose and break down some secondary compounds from leaves (Struhsaker, 2010). Red colobus have a broad distribution range in the African tropical forest region (Struhsaker, 2010; Linder et al., 2021). They are characterized as forest specialists, occupying mature forests with high canopy, but some species (e.g. *Piliocolobus kirkii* and *P. temminckii*) can occupy less forested and drier habitat types (Galat et al., 2009; Galat-Luong, 1983, 1988; Galat-Luong and Galat, 2005; Gatnot, 1975; Siex, 2003; Siex and Struhsaker, 1999; Starin, 1991; Struhsaker, 2010). All habitat types occupied by red colobus species are increasingly under threat of degradation and loss mainly due to anthropogenic activities (Linder et al., 2021) and thus studies of these monkeys across their heterogeneous landscapes are required to better understand their ecological and behavioral adaptations.

Inhabiting heterogeneous landscapes or different habitats triggers variations in activity budget and ranging ecology in intraspecific groups of primates (Chapman and Chapman, 1999; El Alami et al., 2012; Hendershott et al., 2016; Khatun et al., 2018) due to spatial differences in the dispersion and availability patterns of food plant species (Agetsuma and Nakagawa, 1998; Chapman et al., 1997; Chapman and Chapman, 1999; Chapman and Pavelka, 2005; Jones, 2006; Mekonnen et al., 2017; Quintana-Morales et al., 2017; Struhsaker et al., 2004). Several factors influence the activity budget and ranging ecology of primates, including habitat quality, predation risk, intergroup encounters and habitat disturbance (2010; Steel, 2012), but food availability is considered the main factor (Clutton-Brock, 1975; McLester et al., 2019; Rylands, 1986; Struhsaker, 2010). The response of primates to variation in food availability in distinct habitats is very diverse. For instance, variation in food tree density and basal area between sites affect activity budget and ranging ecology of different groups of the same primate species (Stickler, 2004). In Ethiopia, Bale monkeys (*Chlorocebus djambajemensis*) inhabiting a patchy forest spent less time feeding and moving and had a larger home range than those in continuous forests where food trees had larger basal area and bamboo (their main food) density was higher (Mekonnen et al., 2017). In Kibale National Park in Uganda, a group of red-tailed monkeys (*C. ascanius*) in a logged area with lower density and basal area of food trees had larger home range, longer DTD and spent less time feeding than conspecifics in unlogged areas (Stickler, 2004).

Furthermore, primate food resources can vary dramatically in space and between seasons (Brockman and Van Schaik, 2005; Jones, 2006; Tang et al., 2016; Twinomugisha and Chapman, 2008). Especially during the dry season plant foods become scarcer, patchier, and primate diets exhibit lower species richness and diversity (Hemming & Bynum, 2005; Sekulic, 1982). Primates respond to seasonal food fluctuations by adjusting their activity budget, home range size and use, and daily travel distance (DTD) (Hemingway and Bynum, 2005, 2011). For instance, black-fronted titi monkeys (*Callicebus nigrifrons*) in Brazil travelled less in the low-fruit than in the high-fruit season (Nagy-Reis and Setz, 2017) and Assamese macaques (*Macaca assamensis*) in China spent significantly more time resting during the fruit-lean season and more time moving during the fruit-rich season (Li et al., 2020). During the food-scarce season some folivorous primates spent greater amounts of time feeding and moving and consequently increased their home range size or DTD [e.g. eastern lesser bamboo lemurs (*Hapalemur griseus*) in Madagascar: Overdorff et al. (1997); black-and-white colobus monkey (*Colobus guereza*) in Uganda: Harris et al. (2010); Peters' black and white colobus monkeys (*Colobus angolensis palliatus*) in Kenya: Wijiten et al. (2012); Cat Ba langurs (*Trachypithecus poliocephalus*) in Vietnam: Hendershott et al. (2016)], others decreased the time spent moving and increased the time resting [e.g. Sahamalaza sportive lemurs (*Lepilemur sahamalaza*) in Madagascar: Mandl et al. (2018); and white-thighed colobus (*Colobus vellerosus*) in Benin: Djègo-Djossou et al. (2015)], while others did not exhibit seasonal changes in DTD [e.g. Tana red colobus (*P. rufomitratus*) in Kenya: Marsh (1981b); *P. tephrosceles* in Uganda: Isbell (1983) and *L. sahamalaza* in Madagascar: Mandl et al. (2018)], suggesting that other factors apart from food availability influence their activity budget and ranging ecology.

Ashy red colobus monkeys (*Ptilocolobus tephrosceles*), the focal species of our study, occupy diverse habitats ranging from rainforest to dry savanna woodland (e.g. Davenport et al., 2007; Kano, 1971; Nishida, 1972; Rodgers, 1981; Rodgers et al., 1984; Struhsaker, 1975, 2005, 2010, 2016). They occur in western Uganda and Tanzania (IUCN, 2016; Struhsaker, 2010). In Tanzania, the species has been reported in Biharamulo Forest (now Burigi-Chato National Park, southwest of Lake Victoria), Gombe Stream National Park, various parts of the Greater Mahale Ecosystem (including Mahale Mountains National Park) and Mbuzi and Mbizi forests on the Ufipa plateau (2019; Moyer et al., 2006; Ogawa et al., 2004, 2006; Rodgers, 1981; Rodgers et al., 1984). On the Ufipa Plateau, we discovered the presence of Ashy red colobus monkeys in Chala Forest and Ufipa Escarpment, the focal study sites of the present study (Fig. 1; Kibaja et al., 2018; Kibaja, 2022). While Mbizi and Chala are forest reserves, Mbuzi Forest and Ufipa Escarpment are not protected. One population of Ashy red colobus monkeys was reported locally extinct from a forest fragment on the Ufipa Plateau (Davenport et al., 2007) and thus this species may be vulnerable to extirpation due to ongoing habitat modifications outside protected areas. Most sites on the Ufipa plateau are in urgent need of conservation because they occur as insularized habitats due to human activities. These sites are important catchment forests. Our study sites, Chala Forest and Ufipa Escarpment, are priority areas for conservation and research of *P. tephrosceles*, as stipulated in the Conservation Action Plan for African red colobus (Linder et al., 2021). *P. tephrosceles* is classified as an Endangered species because it occurs in isolated populations across its geographical range, and it is threatened with predation by chimpanzees in some protected areas and by habitat alteration in unprotected areas (IUCN, 2016; Lwanga et al., 2011; Linder et al., 2021; Struhsaker and Ting, 2020). Ashy red colobus monkeys are folivorous, feeding predominantly on leaves and supplementing their diet with fruit, flowers, seeds and insects (Struhsaker, 1975, 2010; Kibaja, 2014). Since the species is endangered, its presence in heterogeneous landscapes outside protected areas (e.g. on the Ufipa plateau) can serve as “umbrella” species to conserve sympatric animal and plant species.

Several studies have been conducted on the behavior of Ashy red colobus monkeys in forest and forest mosaic habitats (Chapman and Chapman, 1999; Chapman et al., 2006; Clutton-Brock, 1972, 1975; Gillespie and Chapman, 2001; Isbell, 1983, 2012; Kamenya, 1997; Snaith and Chapman, 2005, 2008; Struhsaker, 1974, 1975, 1980). In Tanzania, they have been studied in forest mosaic habitats, where they are known to utilize both forest and woodland vegetation types (Gombe Stream National Park: Clutton-Brock, 1972; Kamenya, 1997; Stanford, 1998; and Mahale Mountains National Park: Nishida, 1972). Dry savanna woodland habitats currently known to harbor Ashy red colobus monkeys in Tanzania are the Masito and Ugalla regions within the Greater Mahale Ecosystem (Kano, 1971; Moyer et al., 2006; Ogawa et al., 2006; Russak, 2014) and the subpopulation we recently discovered in the Ufipa Escarpment (Kibaja et al., 2018; Kibaja, 2022). All of these dry habitats are dominated by woodland and possess only small and thin strips of evergreen forest vegetation (Hernandez-Aguilar, 2009; Moore, 1994; Pielou, 1952). Prior to this study, no behavioral studies of Ashy red colobus monkeys had been carried out in dry savanna woodland habitat and it was not known how these arboreal and folivorous monkeys could survive in this hot, seasonal and open habitat. To fill this gap in our knowledge, we conducted a study of Ashy red colobus monkey activity budget and ranging ecology in a dry savanna woodland habitat (hereafter savanna woodland). To better understand the strategies of the monkeys in this habitat, we carried out a simultaneous, comparative study in a forest mosaic habitat.

The main aim of our study was to investigate how the different ecological characteristics of a savanna woodland and a forest mosaic habitat influence Ashy red colobus monkey home range use and activity budget. We hypothesized that the forest mosaic habitat would be of higher quality (more young leaves and more concentrated food sources) than the savanna woodland, and that the differential spatiotemporal availability of food sources in the two habitats would influence the monkeys' activity budget and ranging ecology. We

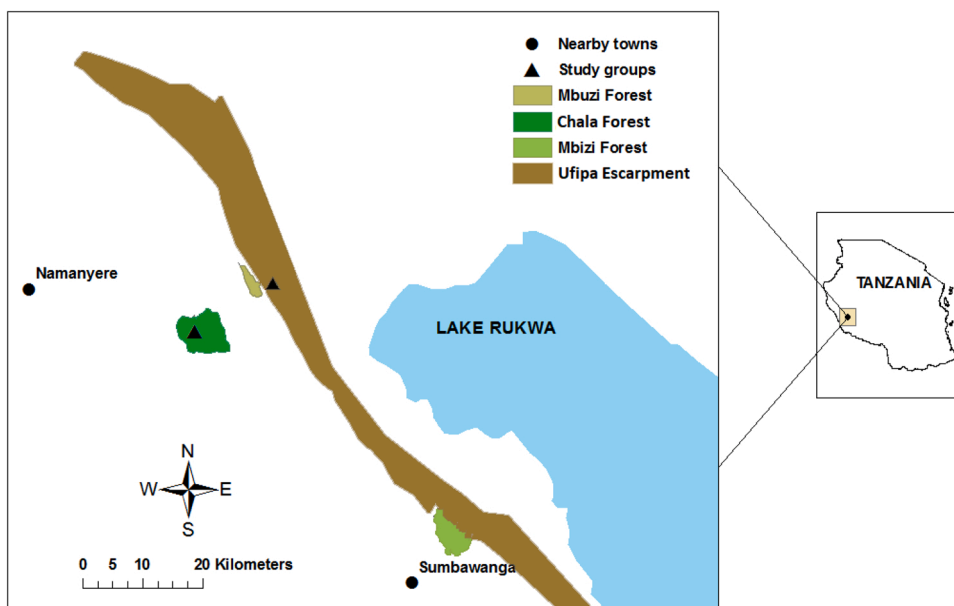


Fig. 1. Location of study sites and groups on the Ufipa plateau.

specifically predicted that: 1) the monkeys would spend more time traveling and feeding in savanna woodland than in forest mosaic; 2) the home range, core areas and mean DTD would be larger for the savanna woodland group than for the forest mosaic group; and 3) DTD would be negatively correlated with availability indices of the monkeys' preferred plant food parts (young leaves and leaf buds), time spent feeding, resting and socializing. We also hypothesized that seasonality would influence activity budget and ranging ecology for both study groups. We predicted that time spent moving, DTD, core areas, and home range would be greater in the dry season than in the wet season for both study groups due to potential food scarcity during the dry season.

2. Methods

2.1. Study area

We conducted our study on the Ufipa Plateau in two sites: Chala Forest and Ufipa Escarpment (Figure 1). The Ufipa Plateau receives 800–1200 mm of annual rainfall (Croon et al., 1984; URT, 2003). Chala Forest (07°34'S, 31°18'E) covers an area of 3395 ha (34 km²) and is managed by the Tanzania Forestry Services (TFS) Agency. It is a forest mosaic habitat dominated by montane forest (where the emergent tree species is *Euphorbia obovalifolia*), but contains also wooded grassland, grassland and woodland vegetation types. Ufipa Escarpment (07°21'S, 31°20'E) is a wall of the Rukwa Rift, west of Lake Rukwa valley. Its steep slope rises from the valley floor at 792 m to an undulating ridge as high as 2438 m, allowing altitudinal zonation of many plant species (Pielou, 1952). We studied the northern section of the Ufipa Escarpment, which is about 40,722 ha (407 km²) and is characterized by a rough terrain dissected by deep gullies. It is a dry savanna woodland habitat dominated by expanses of woodland vegetation type (Pielou, 1952) where the main tree species are *Brachystegia bussei*, *B. utilis*, *Combretum zeyheri*, and *C. mole*. Besides Ashy red colobus monkeys, mammal species present in our study sites include bush pig (*Potamochoerus larvatus*), bushbuck (*Tragelaphus scriptus*), klipspringer (*Oreogtagus oreotragus*), blue duiker (*Philantomba monticola*), leopard (*Panthera pardus*), spotted hyaena (*Crocuta crocuta*), blue monkey (*Cercopithecus mitis*), vervet monkey (*Chlorocebus pygerythrus*), and baboon (*Papio* spp.) (Kibaja, 2022).

2.2. Study subjects

We studied a group of 62 Ashy red colobus monkeys living in savanna woodland habitat in Ufipa Escarpment and another group of 68 individuals inhabiting forest mosaic habitat in Chala Forest. We habituated both groups to the presence of researchers for five months before beginning data collection by following each group from dawn to dusk 5–15 days per month. Neither group was provisioned.

2.3. Data collection

2.3.1. Vegetation description and food availability

To assess food availability, we collected vegetation data within the two groups' home range using randomly located plots of 25 × 10 m for large trees (≥10 cm in diameter at breast height, DBH). The plots were placed within the home range of each study group (covering about 90% of the home range). We counted shrubs, lianas and saplings in 5 × 2.5 m nested plots and estimated the percentage cover of herbs, grasses and forbs in 1 × 1 m nested quadrats (Mligo et al., 2009). We sampled 54 plots in the savanna woodland study site and 22 plots in the forest mosaic study site. The different number of sampled plots in the two different habitats depended on the home range sizes of the group. A higher number of plots was sampled in savanna woodland because the home range of the group living in this habitat was larger than the one living in forest mosaic. For large trees, we recorded the scientific name and DBH (above the buttress for *Ficus* spp.) in centimeters using a vernier caliper. We measured tree crown diameter in meters using a measuring tape. We visually estimated the height in meters. The relative density of leaves in the canopy of each large tree was also visually estimated, and scored using a relative scale from 0 to 5: 0 = no leaves, 1 = 1–20%, 2 = 20–40%, 3 = 40–60%, 4 = 60–80%, and 5 = 80–100% of leaves covering the tree canopy. For those species that could not be identified in the field, we collected samples and dried them for later taxonomic identification by an experienced botanist based at the Herbarium of the University of Dar es Salaam, Tanzania.

For each group's home range, we computed species richness, diversity, stem density and basal area for large trees. We calculated stem density as the number of stems per hectare (ha) and basal area (cm²/ha) of each tree from the DBH recorded using the formula (BA = [0.5 × DBH]² π) (Fashing, 2001a). We computed plant species diversity indices using Shannon diversity indices, *H*, dominance index, *D*, and evenness index, *J* (Krebs, 1999). We used Sorensen's (*S*) index of similarity coefficient to compute plant species similarity between the two habitats using EstimateS (Colwell, 2013). We used PAST v. 3.22 (Hammer and Ryan, 2009) to assess Shannon diversity, dominance, and evenness indices of plant species in each habitat.

For food availability analysis, we used 24-month phenological data for the twelve tree species most frequently consumed by the monkeys in each study site (Kibaja et al. under review). These species accounted for 85.5% and 77.7% of the total time spent feeding by the savanna woodland group and the forest mosaic group, respectively (Kibaja et al., under review). We assessed relative abundance of plant parts: mature leaves, young leaves, leaf buds, flower buds, flowers, unripe fruits and ripe fruits. We scored their abundance using a relative scale from 0 to 4 (0%, 1–25%, 26–50%, 51–75% and 76–100% of the canopy covered by each plant part, respectively) (Gogarten et al., 2014; Struhsaker, 1975). We computed a monthly food availability index (FAI) for each plant part by multiplying the mean phenology scores of a species *i* with mean basal area of species *i* and density of corresponding species *i* per ha (Fashing, 2001a).

2.3.2. Activity budget

MJK and a well-trained research assistant (ML) collected activity data from July 2016 to June 2018. Activities were recorded using scan sampling (Altmann, 1974) during five-minute scans at 15-minute intervals (Bennett, 1986; Mekonnen et al., 2010, 2017) for 5 days each month throughout the study period. The monkeys were followed from dawn to dusk (i.e. 0630–1930). In each scan sample, the activities of the first five visible monkeys from left to right were recorded in order to avoid eye catching activities (Fashing, 2001b; Mekonnen et al., 2010). The activity recorded was that first activity that lasted uninterruptedly for at least 5 s (Struhsaker, 1975, 2010; Marsh, 1981b; Mekonnen et al., 2010). This sampling technique is known as ‘sustained activity’ sampling (Struhsaker, 1975; Marsh, 1981b).

We recorded the following activities: feeding, resting, moving, vocalizing, grooming, mating, aggression, playing and excreting (urinating and defecating). The definitions of activity categories were adapted from previous studies (Bennett, 1983; Marsh, 1981b; Mekonnen et al., 2010). We defined feeding when the monkeys picked and held food with hands or mouth and placed the food into the mouth to chew it. We recorded resting (being inactive) when an individual was found sitting, lying or standing while not engaged in any other major activity category. We recorded moving when individuals were engaged in movements of the whole body rather than just the limbs or other parts of the body. We recorded vocalizing when the subject individual was calling. Grooming was recorded when an individual was engaged in allo-grooming. Mating was recorded when the monkeys were seen copulating. Playing was recorded when the monkeys were seen chasing, wrestling and bouncing each other on branches (social friendly interaction), and aggression was recorded when the monkeys were engaged in physical confrontation between two or more individuals in an aggressive manner.

We obtained a total of 45,069 individual behavioral scan records during 120 days in 24 months of observation for the two groups: 22,513 scans for the savanna woodland group and 22,556 for the forest mosaic group. Since our major goal was to compare the two groups residing in different habitats, we used a combined raw dataset for the 24-month study period for calculating their activity budgets. We computed the proportions of time spent on different activities by dividing the number of behavioral records for each activity category with the total number of activity records. We obtained monthly activity budgets of the groups after averaging the daily activity budgets in a particular month. The grand mean proportions of the monthly budgets provided the total activity budgets for the entire 24-month study period. We merged aggression, grooming, mating and playing into “social” behaviors and also combined vocalizing and excreting behaviors under “other” because these behaviors amounted for < 1% of the total activity budget (Gogarten et al., 2014; Mekonnen et al., 2017).

2.3.3. Home range, core areas and day travel distance

We recorded the location of the estimated geographic center of the study group and elevation using a handheld Garmin GPSMap 64st Geographic Positioning System (GPS) (Bennett, 1983) every 20 min during group follows from dawn to dusk. We estimated home range size using Minimum Convex Polygon (MCP) (Harris et al., 1990) and the Fixed Kernel Density Estimation (KDE) methods (Seaman and Powell, 1996) using all GPS points recorded. We quantified those parameters using a combination of Home Range Tools (HRT) version 2.0 Software (Rodgers et al., 2015) and ArcGIS 10.6.1 (ESRI, 2018). We delineated home ranges as an ad hoc fixed KDE with 95% and 50% isopleths (Mekonnen et al., 2017). We defined home range as 95% KDE and core area as 50% KDE. We also estimated home range using the Minimum Convex Polygon (MCP) method for the purpose of comparison with earlier studies, including 100%, 95% and 90% MCPs.

We determined DTD by converting consecutive dawn-to-dusk GPS points for each group into point shapefiles. We then converted point shapefiles into line shapefiles and measured DTD using Data Management Tools in ArcGIS 10.6.1. The mean DTD travelled by each group was later obtained from the mean of the total 24-month DTD.

2.3.4. Statistical analyses

We used the 24-month dataset for performing all the statistical analyses in R (R Core Team, 2018), employing the lme4 library for random effects and the core library for the rest. We used the Shapiro-Wilk test to examine if the data had a normal distribution. We log transformed day ranging distances and monthly food availability indices and logit transformed the activity budget data (Mekonnen et al., 2017). The transformations were performed in order to fit the assumption of normality before testing for their significant statistical differences.

For each food category (mature leaves, young leaves, leaf buds, flower buds, flowers, unripe fruits and ripe fruits) and for each behavior category (feeding, resting, moving, social and other) we first tested variation between habitats, then for each habitat we tested variation between seasons, using t-tests.

Several of the variables we measured could affect DTD, namely the season, year, habitat, activity budget and food availability. We only have one group per habitat, making the effect of group by itself non-identifiable when habitat is included. Since the effects of habitat and group cannot be disentangled, we did not include group as a possible explanatory variable in the DTD analysis. To explain the variation in DTD, we performed a stepwise search of multiple regression models to explore the set of variables while controlling for variables found to be of significance in previous steps. We performed the analysis in three stages. Stage 1) Since season and year were viewed as nuisance variables, we performed an explorative analysis for these two factors and their interaction. This explorative analysis was performed using a stepwise up search with Bayesian Information Criterion (BIC) as our model selection criterion. Because season is reoccurring, and as such predictive, we handled it as a fixed factor. However, year was deemed non-predictive and was consequently handled as a random effect. The model framework was thus linear mixed-effects models. Stage 2) We tested for the effect of habitat while controlling for the effects from Stage 1 that were found in the stepwise model search. Since we could have started off with a linear mixed-effects model, we used the generally applicable chi-squared likelihood-ratio test for testing new variables, both for the test in this stage and the two tests in the next stage. We wanted a p-value rather than an explorative analysis and this precluded us

Table 1
Vegetation characteristics and plant species diversity indices in the home ranges of our two study groups.

Variables	Savanna woodland	Forest mosaic	df, t, p-values
Number of all large tree species from all plots	54	25	NA
Number of large food tree species from all plots	49	22	NA
All large tree species diversity index, Shannon-Weaver H'	3.05	2.35	395, 6.339, P = 6.32*10 ⁻¹⁰
Large food tree species diversity index, Shannon-Weaver H'	2.95	2.28	394, 6.177, P = 4.71*10 ⁻¹¹
All large tree species evenness index, J	0.39	0.42	NA
Large food tree species evenness, J	0.39	0.44	NA
All large tree species dominance index, D	0.08	0.18	NA
Large food tree species dominance index, D	0.09	0.19	NA
Number of large tree individuals from all plots	449	207	NA
Number of food tree individuals from all plots	433	203	NA
Density of large trees per ha	332.59	376.36	NA
Density of large food trees per ha	320.74	369.09	NA
DBH of all trees (cm)	24.65±(0.67)	30.54±(1.49)	654, 3.553, P = 4.09*10 ⁻⁴
Basal area of all large trees (cm ² /ha)	25420.86±(1464.50)	43566.33±(4923.70)	654, 3.5523, P = 4.1*10 ⁻⁴
DBH of large food trees (cm)	24.99±(0.69)	30.58±(1.51)	634, 3.228, P = 0.001
Basal area of large food trees (cm ² /ha)	26054.37±(159.20)	43753±(5006.40)	634, 3.2282, P = 0.001
Density of saplings per ha	1557.14	1500.00	NA
Density of shrubs per ha	2028.57	300.00	NA
Density of woody climbers per ha	14.29	166.67	NA
Canopy size of all large trees (m)	7.49±(0.20)	6.76±(0.24)	654, -1.118, P = 0.264
Canopy size of large food trees (m)	7.60±(0.20)	6.81±(0.24)	634, -1.400, P = 0.1619
Canopy area of large trees (m ²)	2314.16±(114.11)	1810.22±(143.38)	654, -1.1177, P = 0.264
Canopy area of food trees (m ²)	2372.67±(117.22)	1830.68±(145.74)	634, -1.4004, P = 0.162
Estimate of height of trees (m)	14.08±(0.34)	16.17±(0.54)	652, 3.387, P = 0.0007
Estimate of height of food trees (m)	14.25±(0.35)	16.29±(0.55)	632, 3.234, P = 0.013
Leaf density (Mean percentage)	55.05±(1.14)	45.63±(2.10)	650, -6.0362, P = 2.6*10 ⁻⁹
Herbaceous cover (forbs, grass and non-woody climbers) (%)	51.78±(3.55)	80.91±(5.78)	74, 4.364, P = 0.0023
Height of herbs (forbs, sedges and grasses) (cm)	45.5±(2.41)	72.50±(7.48)	154, 4.3736, P = 2.2*10 ⁻⁵

NA indicates no test was performed. Large trees were those with DBH ≥ 10 cm. Numbers in parentheses indicate standard error, SE of the mean. A significance level of P < 0.05 was considered significant. Gray cells indicate significant results.

from using BIC (see Stage 1). Stage 3) Finally, we tested whether food availability and activity budget affected DTD, while controlling for the effects already found.

We used a significance level of p -value ≤ 0.05 in all statistical inferences. However, since we ran multiple tests when examining the various activities, we Bonferroni-corrected the limit for the p -values to 0.05 divided by the number of activities (five activities). We also Bonferroni-corrected the tests on food items (seven food availability items) the same way.

3. Results

3.1. Vegetation description and food availability

There were very clear differences in vegetation parameters between the forest mosaic and the savanna woodland (Table 1). The Ashy red colobus monkeys used the majority of trees in each habitat as food (savanna woodland: 96.44%, $n = 433$ and forest mosaic: 98.07%, $n = 203$). The species similarity index of all large trees including food trees was low (2 shared species: Sorensen's index = 0.05), indicating that the two habitats are very different. Tree species diversity was significantly higher in the savanna woodland than in the forest mosaic ($t = 6.339$; $p = 6.32 \times 10^{-10}$). The basal area of large trees and of large food trees was significantly greater in the forest mosaic than in the savanna woodland ($t = 3.552$, $p = 4.1 \times 10^{-4}$ and $t = 3.228$, $p = 0.001$, respectively). Tree species richness was higher in the savanna woodland compared to the forest mosaic (54 and 25 tree species, respectively). The density of large trees and of large food trees was higher in the forest mosaic than in the savanna woodland (376.36 versus 332.59 and 369.09 versus 320.74, respectively).

3.2. Activity budget

The group in the savanna woodland spent significantly more time resting (52.48% vs 46.36%, $t = -3.578$, $df = 46$, $P = 0.0008$) and moving (11.32% vs 8.73%, $t = -3.476$, $df = 46$, $P = 0.001$) and less time feeding (30.77% vs 39.94%, $t = 4.644$, $df = 46$, $P = 0.0003$) than the group in the forest mosaic. We did not find significant differences between the group in the savanna woodland and the group in the forest mosaic in the time they spent socializing (5.2% vs 4.8%, $t = -0.289$, $df = 46$, $P = 0.773$) or performing other behaviors (0.3% vs 0.1%, $t = -1.428$, $df = 46$, $P = 0.160$). See Fig. II. Furthermore, we did not find significant seasonal variations in any activity within any group (Table SI).

3.3. Home range, core areas and daily travel distance

The 95% KDE home range for the savanna woodland group was six times larger than for the forest mosaic group (152.53 ha and 25.11 ha, respectively). The 50% KDE core area was also eight times larger for the savanna woodland group than for the forest mosaic group (33.09 ha and 4.15 ha, respectively) (Fig. III and Table 2). The 95% KDE home range was nearly equal in size in the dry (107.55 ha) and in the wet (105.09 ha) season for the savanna woodland group. In contrast, 95% KDE home range for the forest mosaic group was three times larger during the dry (37.82 ha) than during the wet (12.50 ha) season (Fig. IV and Table 2). The forest mosaic group had a nearly five times larger core area in the dry than in the wet season (9.06 ha and 1.90 ha, respectively), whereas the savanna woodland group had core areas of similar sizes in both seasons (23.29 ha and 19.84 ha for the dry and wet season, respectively).

The results of our multiple regression analysis to explain DTD variation revealed that neither season nor year had a statistically significant effect (as judged by BIC in the explorative analysis, Stage 1) on DTD. However, habitat was found to significantly affect DTD

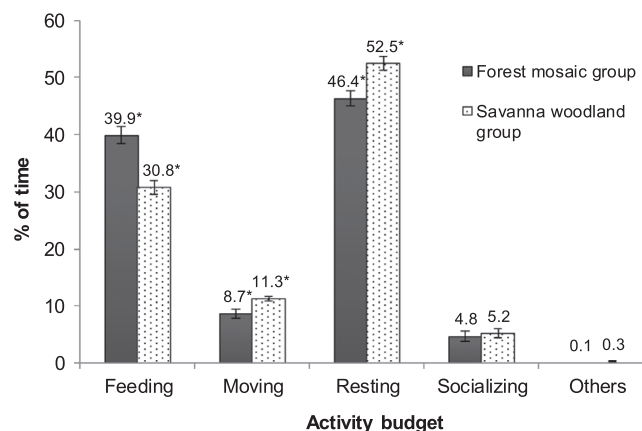


Fig. II. Proportions of time the two study groups of Ashy red colobus monkeys spent in different activities ($N = 24$ months, mean \pm SE; forest mosaic 22,556 scans on 120 days and savanna woodland 22,513 scans on 120 days). * Indicates that pairs are significantly different.



Fig. III. The 24-month home ranges (ha) and core areas (ha) of the two Ashy red colobus monkey study groups in savanna woodland and forest mosaic. Red line (95% MCP), yellow (95% KDE) and green (50% KDE core area).

Table 2

Home range and core area sizes (ha) for the two Ashy red colobus monkey study groups in savanna woodland and forest mosaic.

Group	No. days	Coverage	No. GPS points	100% MCP	95% MCP	90% MCP	95% KDE	50% KDE
Forest mosaic	120	Overall	4348	32.37	27.69	23.92	25.11	4.15
Savanna woodland	120	Overall	4217	179.12	157.51	125.74	152.53	33.09
Forest mosaic	60	Wet	2202	19.64	15.34	11.88	12.50	1.90
		Dry	2146	31.35	31.30	27.20	37.82	9.06
Savanna woodland	60	Wet	2118	148.23	123.95	120.80	105.09	23.29
		Dry	2099	132.49	107.08	85.17	107.55	19.84

($P = 2 \times 10^{-7}$, Stage 2). The savanna woodland group had longer DTD ($520.19 \text{ m} \pm \text{SE } 23.39$, range 141.85–1287 m) than the forest mosaic group ($333.87 \text{ m} \pm \text{SE } 14.97$, range 101.79–912.06 m). Food availability was not found to significantly affect DTD (Stage 3). The smallest p-value for any food source was $P = 0.057$ (for availability of ripe fruits), which is above the Bonferroni-corrected significance limit of 0.007. Neither was activity budget found to have a significant effect on DTD (Stage 3). The smallest p-value was $P = 0.069$, while the Bonferroni-corrected significance limit was 0.01. Since we only found habitat to be significant, we did not test for interactions (extra stage).

4. Discussion

4.1. Impacts of habitat differences on activity budget and ranging ecology

We show that the activity budget and the ranging ecology of Ashy red colobus monkeys remarkably differed in the two habitats we studied. As we predicted, the monkeys spent more time moving in savanna woodland than in forest mosaic habitat. Contrary to our prediction, the monkeys spent less time feeding in savanna woodland than in forest mosaic habitat. As we also predicted, the home range, core areas and mean DTD were larger for the savanna woodland group than for the forest mosaic group. The two habitats we studied differed in abundance of food tree species and plant species composition. The forest mosaic had larger density and basal area of food tree species than the savanna woodland. Contrary to our prediction, we did not detect an influence of food availability indices or activity budget on DTD [Kibaja et al. (in review) report in detail the results of the monthly availability indices of plant parts from phenological data].

We attribute the differences we observed in activity budget, DTD, home range and core area use between our study groups to differences in abundance and distribution of food plant species (but not to the abundance of food plant parts) and canopy gaps within their home ranges. In our study, Ashy red colobus monkeys spent less time feeding and had a larger home range and DTD in savanna

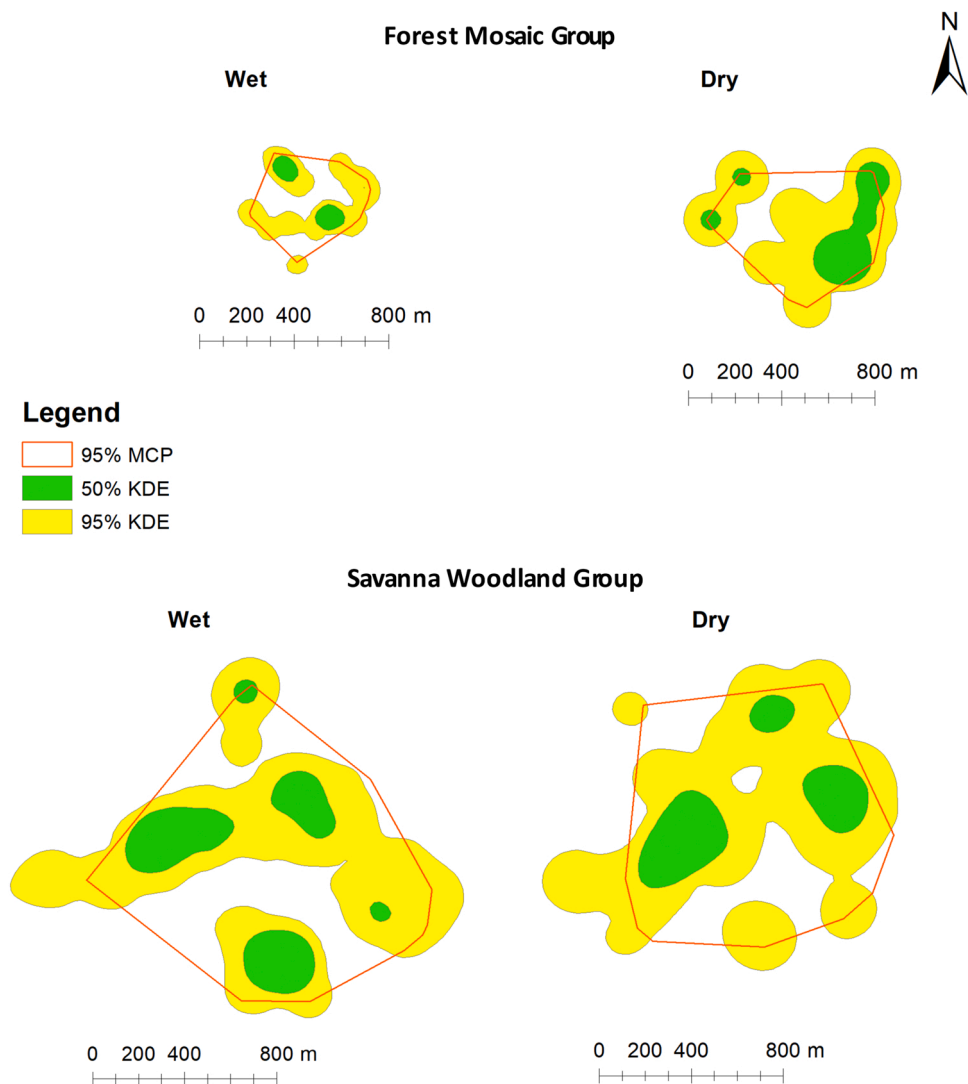


Fig. IV. Seasonal home ranges (ha) and core areas (ha) of the two Ashy red colobus monkey study groups in savanna woodland and forest mosaic. Red line (95% MCP), yellow (95% KDE) and green (50% KDE core area).

woodland where, although plant species richness and diversity were higher, density and basal area of food tree species were lower than in forest mosaic. We suggest that the lower tree species density and basal area might have compelled our group in the savanna woodland to move longer in search of food, thereby increasing DTD, which consequently resulted in a larger home range. Other studies have found the opposite, for instance in Udzungwa, Tanzania, groups of red colobus monkeys (*Piliocolobus gordonorum*) living in sites with higher density of food trees exhibited longer DTD than groups in sites with lower food tree density (Steel, 2012). Furthermore, regarding time spent socializing, a study in Kibale found no difference between groups inhabiting unlogged and logged sites (about 5%), even though they differed in other behavioral aspects (Chapman and Chapman, 1999). Interestingly, in our study, forest mosaic and savanna woodland groups also socialized about 5% of the time (Table SII). Future studies of Ashy red colobus monkeys should consider other variables besides food availability to more adequately identify the factors affecting the activity budgets and ranging patterns in this species.

Variations in basal area and density of food trees result in differences in feeding patch size between the home ranges of conspecific groups (Pruetz & Isbell, 2000). We did not measure patch size in our study, but the greater basal area and density of large trees in the forest mosaic than in the savanna woodland together with our observation that trees were larger and denser in the former habitat, suggest that food patches are larger in the forest mosaic. Large patches would allow the forest mosaic group to feed longer in different vertical levels of the canopy. Furthermore, because feeding patches in the savanna woodland are thin (trees have low density of leaves) and sparse, the monkeys depleted them quickly and needed to keep on the move to search for more food. Not only the feeding patch size, but also the distribution pattern of major food tree species has a strong influence on ranging and behavior. Patchy or clumped distribution of food resulted in large home ranges for Zanzibar red colobus (*Piliocolobus kirkii*) groups in a forest habitat compared to

those in fallow bush habitats (Siex and Struhsaker, 1999; Struhsaker, 2010). We therefore argue that the patchy spatial distribution of food plant species, together with the lower density of food trees and smaller patch size in our savanna woodland site, explain the longer DTD and larger home range size of our study group there compared to our forest mosaic group. Future studies should use the “focal patch method” (Snaith and Chapman, 2005) to investigate the effect of feeding patch size on activity budgets and DTD in our study groups.

Patchy foods may elicit a non-random group movement pattern within the home range (Reyna-Hurtado et al., 2018) or a consistent use of routes leading to potential food locations (Di Fiore and Suarez, 2007; Moore, 1996) in primates. Contrary to the general assumption that folivorous primates travel randomly to exploit their evenly distributed foods (mainly leaves) (Reyna-Hurtado et al., 2018), our data suggest that in habitats with sparsely distributed feeding patches like savanna woodland, folivorous Ashy red colobus monkeys may exhibit a strategy similar to that of frugivorous primates, travelling by using favorite routes to reach widely dispersed patches of preferred food species (Di Fiore and Suarez, 2007). Isbell (2012) showed that DTD increases if there are few routes leading to important feeding sites within the home range. Thus, the presence of few travel ‘arboreal routes’ in open habitats may also force primates to adopt a group movement known as funneling (sensu Isbell, 2012) to reach widely dispersed food patches within their home ranges. Funneling across gaps and moving across logged areas was proposed as a mechanism that increased Ashy red colobus monkeys daily travelling distances in Kibale, allowing them to reach patchy food locations (Isbell, 2012). In the savanna woodland, we observed that the group used the same narrow routes with dense tree stands throughout the study period, avoiding wide gaps in the vicinity, and travelled in subgroups (separated by distances between 30 and 45 m) until they arrived to their destination, where they reunited. When the group travelled to large food patches, several individuals engaged in feeding on-the-go. Sometimes we observed the monkeys moving on the ground. We suggest that the presence of few travel routes in the savanna woodland may partially explain the group’s longer DTD, larger home range size and longer time spent moving in comparison to the forest mosaic group.

4.2. Seasonal variation in activity patterns and ranging ecology

Several studies have reported that primates exhibit seasonal variations in their activity budgets (Doran, 1997; Fonkwo et al., 2015), home range size, and DTD length (Agostini et al., 2012; Guo et al., 2018; Matsuda et al., 2009; Shanee, 2014). Contrary to our predictions, however, we did not find seasonal intragroup variation in the activity budgets of our Ashy red colobus monkey groups. As we predicted, home range and core areas were larger during the dry than the wet season for our forest mosaic group. However, contrary to our prediction, home range and core areas were larger in the wet than in the dry season for our savanna woodland group. Also, contrary to our predictions, we did not find intragroup seasonal variation in DTD. In the forest mosaic habitat, home range and core areas were larger in the dry than in the wet seasons. Despite the large feeding patches in this habitat, young leaves during the dry season decreased, forcing the group to use other parts of the forest for feeding, consequently increasing its home range area and core area. Other red colobus studies, however, reported monthly rather than dry and rainy seasonal variations (e.g. Ashy red colobus monkeys: Isbell, 1983 and Tana red colobus: Marsh, 1981a), probably because these forests do not have a sharp climatic difference between seasons.

The lack of seasonal variation in DTD and activity budget for our savanna woodland group might be due to the elevational distribution and patchy availability of their major food tree species. Regardless of season, Ashy red colobus monkeys repeatedly visited preferred, widely dispersed patches of distinct food plant species (e.g. an evergreen gallery forest, and patches in woodland dominated by *B. bussei* and *B. utilis*). Woodland tree species such as *B. bussei* and *B. utilis* are deciduous, dropping their leaves and flushing up young leaves during the dry season (called “pre-rain green up”) (Ryan et al., 2017; Whitecross et al., 2017). We observed that woodland tree species did not shed their leaves at the same time and individuals within a species produced young leaves asynchronously in the Ashy red colobus monkeys’ home range during the dry season, similarly to what has been reported for other savanna woodland sites in Tanzania (Hernandez-Aguilar, 2006, 2009). This phenomenon allowed our Ashy red colobus group in savanna woodland to use the same parts of the home range in both seasons of the year, potentially explaining the lack of seasonal differences in activity budgets in this group. Future studies should cover different groups in the savanna woodland habitats of the Ufipa and the Greater Mahale Ecosystem in order to learn more about the effect of the pre-rain green up on the ranging and activity budget of this folivorous primate in Tanzania.

4.3. Comparisons of activity budget and ranging ecology of Ashy red colobus and other red colobus monkeys

Although it is difficult to compare the activity budget and ranging ecology of intraspecific groups of primates across habitats and sites because of the different methods used in the studies, it is still worth making such comparisons in order to attempt general explanations for the variation observed (Struhsaker, 2010). Differences in activity budgets and ranging ecology across studies for the red colobus taxa may be attributed to a complex combination of many factors including differences in climate, group size, habitat type, habitat quality, food availability and abundance (Struhsaker, 2010; Steel, 2012). It is difficult to disentangle the effects of such factors in our study.

When comparing our activity budget results to those reported in other studies, it appears that groups of Ashy red colobus monkeys and other red colobus species across Africa spent most of their time feeding and resting (e.g. Clutton-Brock, 1974; Gogarten et al., 2014; Struhsaker, 2010; Marsh, 1981a; Steel, 2012; Fonkwo et al., 2015) (Table SII). Studies have shown that the allocation of substantial amounts of time to resting for some primate species is related to an energy minimization or energy conservation strategy (Mekonnen et al., 2017) and that a long amount of feeding time is related to energy gain (Di Fiore and Rodman, 2001; N’guessan et al., 2009). In our case, we predicted that our savanna woodland group would allocate most time to feeding because of the low abundance

of food tree species in their habitat compared to the forest mosaic group. However, our results did not support our prediction and indicated that the forest mosaic group spent more time feeding than the savanna woodland group. Several other factors may explain differences in activity budget among species of red colobus across their geographical range, including group size, inter-group encounters and methodological differences (Struhsaker, 2010).

The savanna woodland group we studied had the largest home range size ever reported for Ashy red colobus monkeys and other red colobus species (Table SIII; Struhsaker, 2010). This aligns with the findings of larger home range sizes in dry habitats compared to more forested habitats for other intraspecific groups of primates (red-tailed monkeys: McLester et al., 2019; chimpanzees (*Pan troglodytes*): Lindshield et al., 2021). As explained above, the extremely large home range of our savanna woodland group was likely influenced by the patchy distribution of their plant food species and the small size of their feeding patches. As it would be expected based on the spatial distribution of food, the home ranges of Ashy red colobus monkeys living in the forest mosaic habitat of Gombe (Clutton-Brock, 1972; Stanford, 1998; Watt, 1998) are smaller than that of our savanna woodland group and relatively larger than those reported in forest habitats (Table SIII). Several factors may be responsible for differences in the home range size of Ashy red colobus monkey groups, including food quality and predation (see Struhsaker, 2010). With regard to DTD, there is great variation among groups of red colobus taxa (Table SIV Decker, 1994). The largest DTD is the one reported for the Hondohondo group of *P. gordonorum* in the forest habitat of Mwanihana, Tanzania (Steel, 2012) (Table SIV). Further studies on the Ufipa plateau are recommended to study the influence of other factors besides food availability on the activity budget and ranging ecology of Ashy red colobus monkeys.

A limitation of our study was that we studied only one group in savanna woodland and one in forest mosaic. Future studies should include more groups per habitat to confirm if the differences in activity budget and ranging ecology we observed between our two study groups are indeed an effect of habitat type.

4.4. Implications for conservation

In our study, the savanna woodland group utilized a larger home range and travelled longer distances per day than the forest mosaic group. To travel, the savanna woodland group depended on narrow arboreal routes made up of connected dense tree stands, which are few and not uniformly distributed across its home range. The group consistently utilized these arboreal routes when it moved between woodland and evergreen gallery vegetation types and vice versa. Illegal selective tree cutting in the area (Kibaja, 2022; Kibaja et al., 2018) will not only remove habitat connectivity, lowering the number of patches of potential food plant species the monkeys could exploit, but will also decrease overall species richness and diversity of food plants for the monkeys. Based on our findings, we conclude that the effective conservation of Ashy red colobus monkeys in savanna woodland habitats needs the designation of large, protected areas (e.g. a national park, game reserve or forest reserve) to ensure the maintenance of their food resources and traveling routes. Specifically in the Ufipa plateau, our study region, we call for the whole Ufipa Escarpment to be protected as a community owned conservation area, as currently the only protected sites are Mbizi and Chala forests.

The forest mosaic group we studied occurs in an elongated evergreen forest patch naturally isolated from other pockets of evergreen forest (not occupied by the monkeys) by an area of montane wooded grassland about 1 km thick surrounding the patch. The group did not use the entire forest patch, but rather utilized a small part of it as its home range. Members of this forest mosaic group engaged longer feeding times than the savanna woodland group and in most cases maximized food intake by foraging in the dense understory intertwined with climbers and herbs about 3 m from the ground (Kibaja et al. in review), making them vulnerable to interact with waste left by human and domestic animals (e.g. feeding remnants and feces), and consequently potential parasites and novel pathogens. The monkeys were seen on occasion running on the ground through a trail to reach nearby trees and therefore they can potentially forage on the ground, a behavior that can expose them to the risk of pathogen disease transmission (Kurpiers et al., 2016; Paige et al., 2014; Wolfe et al., 2005). We found that our forest mosaic group had gastro-intestinal parasites that infect humans (González-Moreno et al., 2020), opening the possibility that the monkeys may have acquired these parasites from humans.

A study showed that there has been local extinctions of Ashy red colobus monkey subpopulations on the Ufipa Plateau (Davenport et al., 2007) and thus it is essential to protect the remaining subpopulations. Chala Forest is protected by the Tanzania Forests Services Agency (TFS) as a forest reserve, although selective logging and poaching activities are not uncommon. The Ufipa Escarpment offers hope for the long-term persistence of Ashy red colobus monkeys and other mammals because its steep and rugged terrain prevents traditional agriculture and therefore provides a relatively safe refuge. The Sumbawanga District Council manages the Ufipa Escarpment as a catchment, but its protection category is unclear because there are parts of the escarpment traditionally reserved by local people as village forest reserves. In addition, secretive illegal growing of marijuana (*Cannabis sativa*) takes place. We recommend increased community conservation participation and education in the two study sites to ensure co-existence between monkeys and the local community. Community involvement should focus on afforestation programs in surrounding villages in order to reduce illegal exploitation of trees in both study sites to ensure the long-term persistence of monkeys in these threatened habitats.

Ethical note

This research was noninvasive, complied with the Guidelines of Best Practices for Field Primatology of the protocols of the International Primatological Society, adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates and to the legal requirements of Tanzania. The authors declare no conflict of interest.

Funding

This work was supported by Rufford Foundation, International Primatology Society (IPS), Barcelona Zoo Foundation, Fresno Chaffee Zoo, Center for Ecological Evolutionary Synthesis (CEES), and Norwegian State Educational Loan Fund (Quota Scheme, Norway).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data set analyzed in our study is available from the corresponding author on reasonable request.

Acknowledgements

We are grateful to Thomas T. Struhsaker, Lynne A. Isbell, Kim McConkey and to two anonymous reviewers for their insightful comments that greatly improved this manuscript. We thank the Norwegian State Quota Scholarship Program for funding MJK PhD program at the University of Oslo. We grateful to Rufford Foundation, International Primatology Society (IPS), Barcelona Zoo Foundation, Fresno Chaffee Zoo and the Center for Ecological and Evolutionary Synthesis (CEES) for generous funding to MJK for conducting this study. RAH-A is grateful to the Serra Hunter Programme for support. We thank the Tanzania Wildlife Research Institute (TAWIRI) for granting permission to conduct this research. We also thank the Sumbawanga District Council and the Tanzania Forests Services (TFS) Agency for logistical support. Special thanks go to our field assistants for their hard work: Herman Dominick, Leonard Ernest, James Siumbu, Frank Nkalasa and Daud Ndasi. We are grateful to Yahya Abeid for the taxonomic identification of plant specimens. We also thank the village executive officer and environmental committee from the Mfinga village in Sumbawanga District for allowing us to work in their districts' areas.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02440](https://doi.org/10.1016/j.gecco.2023.e02440).

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