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ORIGINAL ARTICLE

Population size and habitat preference of the Omo River guereza (*Colobus guereza guereza*) in a multi-habitat matrix in the central highlands of Ethiopia

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Abstract

Given the current rate of habitat degradation and loss in the tropics, data on primate population densities and habitat use are indispensable for assessing conservation status and designing feasible management plans for primates. The Omo River guereza (*Colobus guereza guereza*) is a subspecies of the eastern black-and-white colobus monkey endemic to the western Rift Valley forests of Ethiopia. Their restricted distribution along with habitat loss and hunting within their range render them vulnerable to local extirpation and extinction. Furthermore, there are no published data available on the population status and habitat use patterns of the Omo River guereza. We therefore aimed to assess the population size of Omo River guerezas in different habitats (*Erica-Juniperus* mixed forest, mixed plantation forest, undisturbed natural forest, disturbed natural forest) using transect surveys at Wof-Washa Natural State Forest (WWNSF) in central Ethiopia. Our surveys covered a cumulative distance of 88.5 km in four different habitats, during which we recorded a total of 140 Omo River guereza groups. The average group density was 14.3 groups/km^2, average individual density was 94.4 individuals/km^2, and we estimated the total population size within WWNSF to be 2549 individuals. The sex ratio of the population was split evenly between males and females, though the age classes skewed strongly towards adults. Of the habitats surveyed, the highest group encounter rate (1.83 groups/km) occurred in the disturbed natural forest. However, the highest individual density (110.1 individuals/km^2) was recorded in undisturbed natural forest. Still, sizable densities (group and individual) were recorded in three of the disturbed habitats (disturbed natural forest, mixed plantation forest, and to a lesser extent *Erica-Juniperus* mixed forest). Our study offers the first baseline information with which to compare future population density estimates and habitat use in the range of Omo River guerezas.

Keywords Anthropogenic disturbance · Black-and-white colobus monkey · Census · Colobine · Wof-Washa Natural State Forest

Introduction

Primates are considered to be among the most threatened mammal groups worldwide, an unfortunate status largely due to a variety of anthropogenic pressures (Schipper et al. 2008; Estrada et al. 2017, 2020). Throughout the tropics, these negative anthropogenic pressures often include agricultural/human settlement expansion and resource extraction, resulting in habitat loss, fragmentation, and degradation (Fahrig 2003; Hansen et al. 2013; Laurance et al. 2014). In effect, deforestation reduces or eliminates key resources (Marsh and Chapman 2013; Almeida-Rocha et al. 2017; Estrada et al. 2017), forcing primates to cope by shifting their feeding and ranging ecology, or alternatively to become locally extirpated (Chapman et al. 2010; Bracebridge et al. 2012; Mekonnen et al. 2018).

Most primate species display microhabitat preferences, occupying specific forest strata or habitat types (Rendigs et al. 2003; Porter 2004; Campbell et al. 2018). Ecological factors such as forest structure, habitat area, and spatial and temporal resource availability are critical in determining the distribution of primate species (Arroyo-Rodríguez and Mandujano 2009; Campera et al. 2014; Galán-Acedo

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et al. 2019a). Of particular interest are endemic species (i.e., those occurring in a single country or region), as they typically have smaller populations across a more restricted area. Endemics are thus more susceptible to extinction than non-endemics (Lamoreux et al. 2006; Estrada et al. 2018; Mekonnen et al. 2020). Therefore, determining the full geographic distribution of primate species allows for effectively pursuing specific conservation actions and identifying priority areas for species conservation (Bersacola et al. 2018; Heinicke et al. 2019).

Ethiopia, like most of Africa, has experienced significant recent forest loss due to agricultural and grazing land expansion, monoculture plantations, and resource extraction for fuel wood/charcoal production (Ameha et al. 2014; Mekonnen et al. 2020). The majority of the remaining forest patches in Ethiopia persist near religious centers, and within inaccessible and/or protected areas (Alelign et al. 2007; Wassie 2007). Moreover, the natural resources within these forests have been steadily declining in size and quality (Alelign et al. 2007; Wassie 2007). These human-induced effects on resources and habitat area can affect the survival of Ethiopia's endemic primate species through isolating populations, potentially increasing predation, reducing genetic diversity, and disrupting gene flow (Anderson et al. 2007; Bergl et al. 2008).

One primate taxon of particular interest in Ethiopia is the guereza (*Colobus guereza*; also referred to as the black-and-white colobus monkey). Although the species as a whole is geographically widespread across equatorial Africa (Fashing 2001a; Chapman et al. 2007), two range-restricted subspecies of guerezas are endemic to Ethiopia, the Omo River guereza (*C. g. guereza*, Rüppel 1835) and the Djaffa Mountains guereza (*C. g. gallarum*, Newmann 1902) (Fashing and Oates 2013; Zinner et al. 2019).

Guerezas are relatively large, arboreal, and diurnal monkeys, and have been studied in large contiguous rainforests as well as in gallery forests and fragments, where they often reach exceptionally high population densities and occupy exceedingly small home ranges (Oates 1977a; Dunbar 1987; Fashing 2022). They are considered highly folivorous, with a diet usually consisting mostly of young leaves (Oates 1977a; Wasserman and Chapman 2003; Tesfaye et al. 2021). However, some populations exhibit dietary flexibility by consuming fruits in large quantities when available (Fashing 2001b; Plumptre 2006).

Relatively little research has been carried out on guerezas in Ethiopia (Dunbar and Dunbar 1974; Dunbar 1987; Tesfaye et al. 2021) despite a notable decline in distribution and abundance due to forest clearance and hunting during the latter half of the twentieth century (Dunbar and Dunbar 1975; Yalden et al. 1977). Population density estimates and up-to-date inventories of key areas are critically important to determine the overall health of primate communities (Plumptre et al. 2013). Furthermore, understanding population dynamics is crucial to developing effective conservation management plans (Lwanga et al. 2011).

Given the paucity of current population data for guerezas in Ethiopia, we aimed to determine the population size and habitat preferences of one subspecies, the Omo River guereza (*Colobus guereza guereza*), in a multiple-use protected area, Wof-Washa Natural State Forest (WWNSF), in the central highlands of Ethiopia. Because guerezas are known to be adaptable monkeys (Oates 1977a; Fashing 2022) and previous studies of Omo River guerezas have shown that the subspecies relies on a mixed diet of mostly leaves and some fruit (Dunbar and Dunbar 1974; Tesfaye et al. 2021), and because mixed diets appear to allow for greater ecological flexibility (Eppley et al. 2020), we predicted that guerezas would be widespread throughout WWNSF across a variety of habitats. Though we predicted that guerezas would be encountered throughout WWNSF, we also predicted that their population would have similar density estimates across different habitats. Lastly, we predicted that the site would have a similar number of females and males, as hunting of guerezas is prohibited by the cultural traditions of the people in the central highlands of Ethiopia.

Methods

Study site

WWNSF is located in the North Shewa administrative zone of Amhara National Regional State, in the central highlands of Ethiopia (Fig. 1). The escarpment forms part of the catchment of the Awash River system which drains into the Danakil plains in the northern section of the Rift Valley (Bekele 1993). This protected area provides the only stretch of forest remaining in the surrounding landscape, extending between approximately 9°42′–9°47′ N latitude and 39°43′–39°49′ E longitude (Fig. 1). WWNSF is one of the very few remaining dry Afromontane forests and is one of the oldest natural state-owned forests within the eastern Afromontane hotspot, extending across much of the Ethiopian highlands and containing high levels of biodiversity and species endemism despite escalating habitat threats (Mittermeier et al. 2005). The vegetation of WWNSF can be described as dry evergreen Afromontane forest mixed with both broadleaf and conifer forest along the eastern escarpment of the northwestern highlands, with an ericaceous belt at higher altitudes (Friis et al. 2011). In total, there are over 394 plant species at WWNSF, of which 46 species (12%) are endemic to Ethiopia (Teketay and Bekele 1995; Ayalew 2018). The cliffs and steep slopes of the highland terrain make building

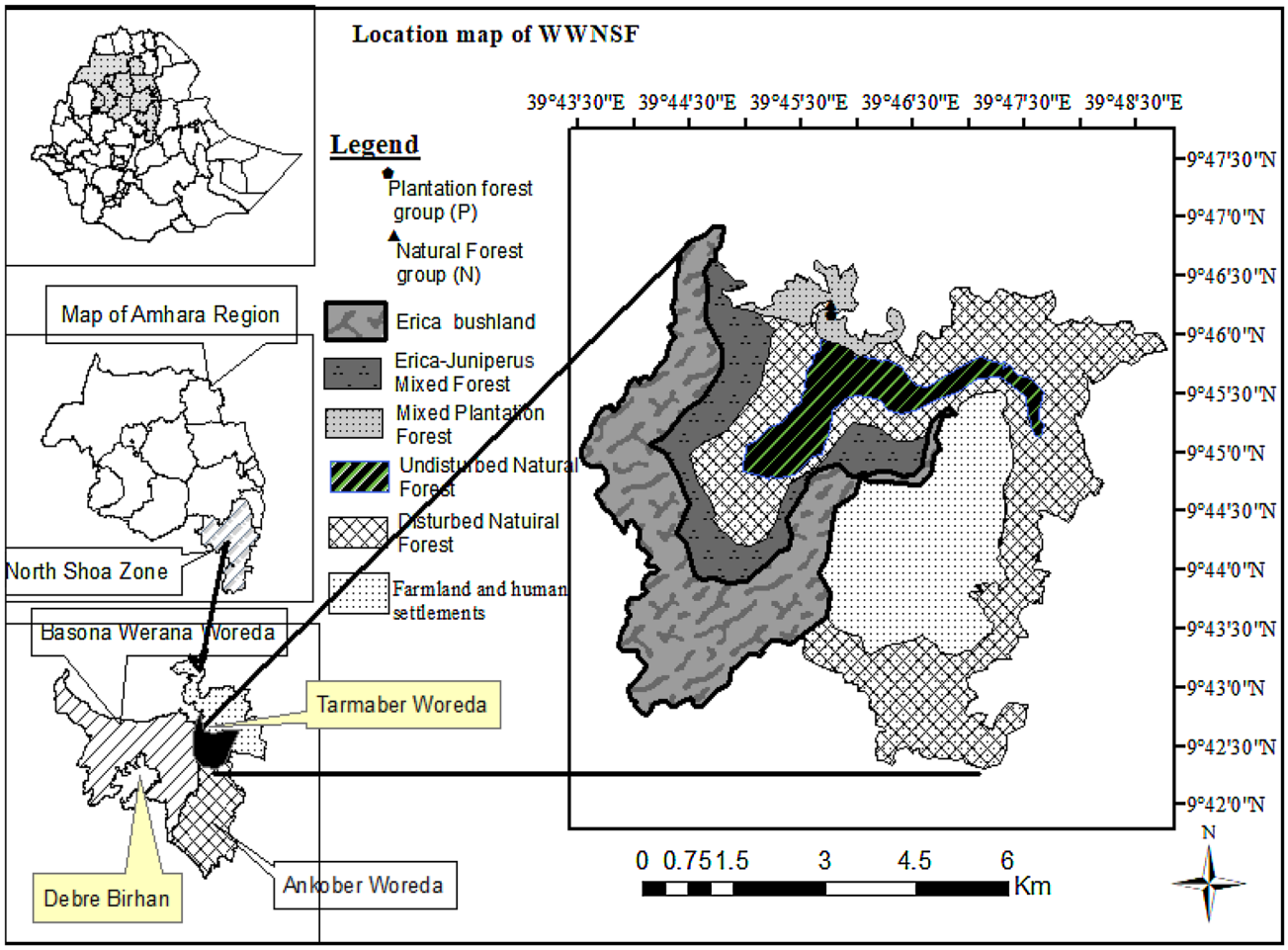

Fig. 1 Map of the study area, Wof-Washa Natural State Forest, Ethiopia and the habitat types contained within it

roads into and through the forested area nearly impossible. Thus, the inaccessibility of the area, even on foot in places, has enabled most of the original tree population to persist (Yirga et al. 2019).

We classified WWNSF into five habitat types based on the dominant vegetation types and disturbances (Table 1). These habitats are *Erica* bushland (EBL = 1139 ha), *Erica-Juniperus* mixed forest (EJMF = 485 ha), mixed plantation forest (MPF = 130 ha), undisturbed natural forest (UDNF = 317 ha), and disturbed natural forest (DNF = 1628 ha), which altogether cover 3699 ha (Fig. 1). The calculated area of each habitat type was obtained through digitization in Google Earth and excludes the area covered by steep escarpments (i.e., cliffs) and human settlements within the forest.

In addition to Omo River guerezas, the study area supports several large predators (e.g., *Panthera pardus*), primates (e.g., *Chlorocebus aethiops*), ungulates (e.g., *Tragelaphus scriptus meneliki* and *Oreotragus oreotragus*), and a variety of birds, amphibians, and reptiles (Negesse 2017).

Data collection

During reconnaissance surveys in February to April 2015, we selected study sites to cover a range of altitudes and habitat types. We then conducted a detailed population survey of Omo River guerezas in WWNSF from February 2015 to April 2016. Four of the five habitat types were chosen for surveys, with only EBL excluded because it lacked the tree cover necessary to provide habitat for guerezas. We established line transects based on a stratified random sampling approach within different habitat types and marked every 50 m interval using flagging tape (Chapman et al. 1988; Rovero et al. 2006; Mammides et al. 2008). Across the four survey habitat types, a total of 13 transects were created, with each ranging from 1.5 to 3.0 km in length. Transect width varied from 40 to 80 m on either side of the transect due to the variation in the nature of the vegetation in each

Table 1 Description of the five habitat types within Wof-Washa Natural State Forest, Ethiopia

Habitat type	Abbr.	Elevation	Description
Erica bushland	EBL	≥3100 m	Dominated by genus *Erica*, a small shrub within the family Ericaceae, and where trees are rare or absent and graminoids and forbs are common
Erica-Juniperus mixed forest	EJMF	2510–3100 m	Mixed-forest tree species with a high co-occurrence of *Erica* and *Juniperus* trees and mostly open canopy
Mixed plantation forest	MPF	2510–3100 m	Non-natural forest established by planting and/or seeding trees for the process of afforestation or reforestation. Consists of two or more introduced or indigenous tree species successfully co-existing in a low diversity forest
Undisturbed natural forest	UDNF	2510–3100 m	An intact natural forest of native flora species, where there are no clear visible indications of human activities. The most common tree species include *Podocarpus falcatus* (Podocarpaceae), *Juniperus procera* (Cupressaceae), *Maesa lanceolata* (Primulaceae), *Hagenia abyssinica* (Rosaceae) and *Polyscias fulva* (Araliaceae)
Disturbed natural forest	DNF	2510–3100 m	Forest type with native and introduced tree species occurring in a degraded state due to past and present human activities. The most common tree species include *Juniperus procera*, *Allophylus abyssinicus*, *Maesa lanceolata*, *Cupressus lusitanica* and *Olinia rochetiana*

Abbr Abbreviation/acronym

habitat and resulting visibility (i.e., fall-off distance): 40 m on either side of the transect in UDNF, 50 m in MPF, 60 m in DNF, and 80 m in EJMF. Surveys were conducted from 06:30 to 10:45 in the morning and from 14:00 to 18:00 in the afternoon so as to coincide with the activity periods of the study species (Mekonnen et al. 2010; Chagas and Ferrari 2011). Transects were walked at an average speed of 1 km/h, and we paused at regular intervals to scan the forest and listen for vocalizations and movements in the canopy (Fashing and Cords 2000; Mekonnen et al. 2010).

When we encountered guerezas along a transect, we recorded the animal–observer distance (m), sighting angle (angle to trail using a compass), perpendicular distance (m) from the transect to the first animal seen, the height (m) of the tree where the animal was first detected, group spread (radius) (m), group size, the dominant habitat type, global positioning system (GPS) coordinates, and elevation (m) of the area (Rovero et al. 2012; Chagas and Ferrari 2011; Lwanga et al. 2011). We used a Nikon 550 range finder to estimate the animal–observer distance and Suunto A-10 compass to estimate the sighting angle. We assigned each observed individual to one of the following age/sex classes based on relative body size and coloration: adult male, adult female, subadult male, subadult female and juvenile (Fashing 2001b; Wong and Sicotte 2006). We spent a period of up to 30 min with each encountered group to determine the age-sex composition and group size as reliably as possible given the time limitations inherent in conducting transect surveys (Struhsaker 1981; Fashing and Cords 2000). Sex of individuals was determined by differences in body morphology and genitals, and/or by the large continuous horizontal line of white hairs found across the perineum of males (Fashing 2001a). We considered individuals within 50 m of one another to belong to the same group (Whitesides et al. 1988). We acknowledge that group counts collected during surveys may be incomplete due to the limited time spent with each group, as well as the complex forest structure and steep topography that truncated observer visibility (Plumptre and Cox 2006; Marshall et al. 2008; Mekonnen et al. 2020). Nevertheless, we did our best to spot all individuals within 50 m of the first individual sighted.

Data analyses

We calculated encounter rates of groups per kilometer for each habitat type (Bobadilla and Ferrari 2000), and summarized sightings as the total number of individuals and groups observed in each habitat type (Anderson et al. 2007). Because our data did not always conform to the assumptions of distance sampling (Plumptre et al. 2013), we calculated densities by dividing the number of observations by the corresponding habitat area (sum of the total transect length multiplied by transect width) (Struhsaker 1981; McLester et al. 2019). We calculated group density of guerezas in each habitat type by summing the number of groups observed in each habitat, divided by each habitat's area. We estimated population density by multiplying group density estimates with the observed mean group size (total number of individuals divided by total number of groups in the survey) of guerezas (Fashing and Cords 2000; Mekonnen et al. 2010). Lastly, total population size was estimated by multiplying the average group density estimates with the mean group size and the total area of the corresponding suitable habitat in the study site (Chiarello 2000; Mekonnen et al. 2010). We conducted all statistical tests using IBM SPSS 26 (George and Mallery 2019). Furthermore, Kruskal–Wallis *H* tests were used to examine individual, group, and population density differences based on habitat use preferences, while

Mann–Whitney *U* tests were used to examine differences in sex and age structures. Statistical significance was set at $P \leq 0.05$.

Results

Population estimates

A total of 140 guereza groups were recorded over 39 transect surveys across 88.5 km. The average group encounter rate of guerezas along transect lines was 1.52 ± SD 0.22 groups/km (range 1.33–1.83 groups/km) (Table 2). The highest encounter rates were recorded in the DNF (1.83 groups/km) and MPF (1.47 groups/km), while the lowest encounter rates were recorded in the EJMF (1.33 groups/km) (Table 2). Still, there were no statistical differences in the group encounter rates across all the transects during the survey period (Kruskal–Wallis test $\chi^2 = 12$, df = 12, $P = 0.446$).

Group size at WWNSF varied from 3 to 16 individuals, with a mean group size of 6.8 ± SD 0.4 individuals (Table 2). Mean group size varied slightly between habitat types, ranging from a low of 6.2 in UDNF to a high of 7.1 in MPF (DNF 7.0, EJMF 6.8). The mean group density of guerezas was 14.3 ± SD 4.4 groups/km^2 (range 8.3–18.9 groups/km^2), while the mean individual density was 94.4 ± SD 25.2 individuals/km^2 (range 56.8–110.1 individuals/km^2) (Table 2). UDNF was the habitat with the highest individual density (110 individuals/km^2), followed closely by DNF (107 individuals/km^2) and MPF (104 individuals/km^2), and more distantly by EJMF (57 individuals/km^2). There were no statistical differences in mean individual density between the different habitat types (Kruskal–Wallis test $\chi^2 = 3$, df = 3, P = 0.39). Within WWNSF, the total area of tree-dominated forest habitat habitable for guerezas was 27 km^2. The total population size of guerezas in WWNSF was estimated to be 2549 individuals.

With regard to altitudinal distribution, we found that guerezas were most abundant between 2510 and 3100 m asl (above sea level) ($n = 842$, 88.4%), which corresponds to the dry evergreen Afromontane forest ecosystem. Abundance was lower at altitudes above 3100 m asl ($n = 110$, 11.6%) (Fig. 2).

Age and sex composition

The mean number of guereza individuals observed in the 140 groups sighted during the surveys was 317 ± SD 16.29, with 225 categorized as adults and 69 as subadults (Table 3). Juveniles and infants accounted for 16 and 7

Table 2 Omo River guereza survey data from transects conducted in each habitat type at WWNSF

Habitat types	No. Tn	Tn.L (km)	SW (km)	Survey months				Dist. surveyed (km)	T. gp. no	Gp. enc rate	Mean gp size	Gp. density	Pop. density (Ind./km^2)
				May 2015		Sep. 2015		Jan. 2016					
				Gp. no	T. Ind	Gp. no	T. Ind	Gp. no	T. Ind				
MPF	2	5.0	0.10	6	45	6	43	10	68	15.0	22	1.47 ± 0.8	7.1 ± 1.1	14.67 ± 7.5	104.0 ± 67.8
EJMF	2	5.5	0.16	7	53	7	49	8	48	16.5	22	1.33 ± 0.2	6.8 ± 0.9	8.33 ± 2.4	56.8 ± 23.6
DNF	6	12.0	0.12	21	143	21	151	24	167	36.0	66	1.83 ± 0.7	7 ± 0.7	15.28 ± 6.1	106.7 ± 38.1
UDNF	3	7.0	0.08	11	65	10	67	9	53	21.0	30	1.43 ± 0.1	6.2 ± 0.8	18.86 ± 1.4	110.1 ± 21.2
Overall total	13	29.5		45	306	44	310	51	336	88.5	140	1.52 ± 0.2	6.8 ± 0.4	14.29 ± 4.1	94.4 ± 25.2

Note: *No. tn.* number of transects, *Tn. L* transect length, *SW* strip (sighting) width, *Gp. no.* group number, *T. ind.* total individuals, *Dist.* distance, *T. gp. no.* total group number, *Gp. enc. rate* group encounter rate, *MPF* mixed plantation forest, *EJMF Erica-Juniperus* mixed forest, *DNF* disturbed natural forest, *UDNF* undisturbed natural forest

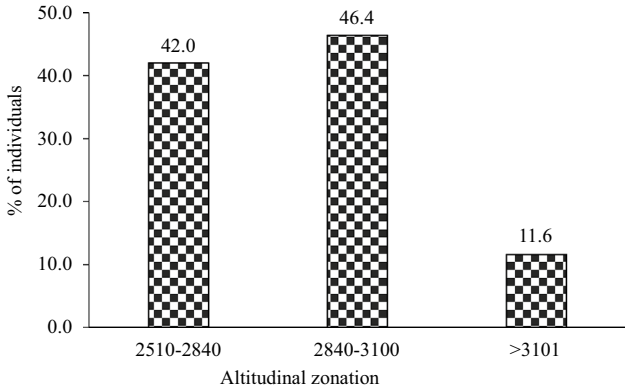

Fig. 2 Percentage of total Omo River guerezas sighted ($n = 952$) across the three altitudinal zones at Wof-Washa Natural State Forest, Ethiopia

individuals, respectively. Considering sex composition, females constituted an average of 32.0 ± 9.2 (52%) individuals, while males averaged 29.5 ± 9.3 (48%) individuals. The overall average sex ratio between males and females was 1.0:1.1 and did not differ significantly across habitat types within WWNSF (Mann–Whitney *U* test, $W = 11$, $P = 0.471$). During the surveys, more adult individuals were recorded than subadults and young for both sexes. The overall average subadult to adult age ratio was 1.0:3.3. A Mann–Whitney *U* test revealed a significant difference ($W = 15.5$, $P = 0.041$) in the age distribution of guerezas in the study area. Only four of the guereza groups observed contained multiple adult males, all of them recorded in January 2016. All-male groups were never observed during the surveys.

Discussion

Our results demonstrate that Omo River guerezas in WWNSF appear to have a relatively small, localized population in rapidly degrading tropical forest with a high ratio of adults to immatures. Our surveys revealed a mean group density of 14.3 groups/km^2 (Table 4). Because mean group size (6.8 individuals) at WWNSF was rather low, however, mean individual density was moderate relative to other guereza populations (Table 4). Guereza density was comparable in UDNF, DNF, and MPF, but much lower in EJMF, and guerezas appeared to be absent from EBL, where there is limited tree coverage and little potential food supply for guerezas (Table 2). Because the abundance and distribution of food sources are major influences on primate abundance (Chapman et al. 2003; Hanya and Chapman 2013), it is not surprising that guerezas are scarce to absent in EJMF and EBL. Unlike with densities, group sizes were comparable in all four habitat types where guerezas occurred (Table 2).

Table 3 Age and sex classes of Omo River guerezas in the four different habitat types where they occur in WWNSF

Habitat type	Total	AM	AF	UA	SAM	SAF	USA	Juv	Inf	M	F	Ad	Sa	Sa:Ad	M:F
MPF	52	15	17	5	4	3	3	2	2	19	20	37	11	1:3.4	1:1.1
EJMF	50	14	16	4	4	5	4	3	2	17	21	34	12	1:2.8	1:1.2
DNF	154	46	48	13	10	12	12	10	2	57	59	107	34	1:3.2	1:1.1
UDNF	62	20	23	4	5	5	3	2	1	25	28	47	12	1:3.9	1:1.1
Total	317	96	103	26	23	25	21	16	7	118	128	225	69	1:3.3	1:1.1
Mean ± SE		23.8 ± 7.5	26 ± 7.5	6.5 ± 2.2	5.8 ± 1.4	6.3 ± 2	5.5 ± 2.2	4.3 ± 1.9	1.8 ± 0.3	29.5 ± 9.3	32 ± 9.2	56.3 ± 17.1	17.3 ± 5.6		
Percentage		30.3	32.5	8.2	7.3	7.9	6.6	5.0	2.2	48.0	52.0	71.0	21.8		

Note: *AM* adult male, *AF* adult female, *UA* unidentified adult, *SAM* subadult male, *SAF* subadult female, *USA* unidentified subadult, *Juv* juvenile, *Inf* infant, *M* male, *F* female, *Ad* adult, *Sa* subadult

Table 4 Encounter rates, densities, mean group sizes, adult sex ratios, and study sites of *Colobus guereza* subspecies across Africa

Subspecies	Population density (ind/km^2)	Group density (Grps/km$^{2)}$	Mean group size	AF:AM	Elevational range (m)	Study site	Habitat occupied	Source
C. g. guereza	94	14.3	6.8	1.1	2510–3100	WWNSF, Ethiopia	Afromontane forest	This study
C. g. matschiei	168	11.7	14.4	1.6	1580	Kakamega Forest, Kenya	Mid-elevation rainforest	Fashing et al. 2012
C. g. matschiei	109	11.2	9.7	–	1580	Kakamega Forest, Kenya	Mixed plantation forest	Fashing et al. 2012
C. g. occidentalis	347	43.4	8.0	4.5	1150	Kyambura Gorge, Uganda	Fragmented riverine forest	Kruger et al. 1998
C. g. occidentalis	100	8.8	11.4	2.4	1500	Kibale Forest, Uganda	Mid-elevation rainforest	Oates 1977b
C. g. occidentalis	17	1.2	13.9	–	600–1200	Ituri, D. R. Congo	Lowland riverine rainforest	Bocian 1997
C. g. occidentalis	49	7.1	6.9	3.3	1100–1600	Budongo, Uganda	Mid-elevation rainforest	Suzuki 1979

Further, guereza groups exhibited no significant sex bias, with relatively even male–female sex distributions in each habitat type. However, the high ratio of adults to immatures suggests poor juvenile recruitment in the guereza population at WWNSF and is cause for long-term conservation concern.

Our finding of robust densities for guerezas across most forest types at WWNSF is consistent with patterns for guerezas at other study sites across East Africa (Fashing and Oates 2013). Guerezas generally fare as well or better in disturbed forest as in undisturbed forest, suggesting they are unusually flexible ecologically for an arboreal primate species (Oates 1977a, b; Dunbar 1987; Fashing and Oates 2013). Recent research from southern Ethiopia demonstrated that guerezas modify their diet considerably to cope with disturbance and modification to their habitat (Tesfaye et al. 2021). Furthermore, within Kibale National Park, Uganda, this guereza did not show any measurable behavioral differences based on proximity to anthropogenic or natural forest edges (Hodder and Chapman 2012). Still, there is an intensity of habitat disturbance and modification with which even guerezas cannot cope, as demonstrated by Chapman et al.'s (2007, 2013) longitudinal study of guereza population decline and extirpation in small fragmented forests in western Uganda.

Our study at WWNSF suggests that guerezas generally do well in UDNF, DNF, and MPF, but far less well in EJMF, and are unable to survive in EBL. The MPF, in particular, covers only a small portion of WWNSF and the population density reached there could be an outcome of population compression (Dunbar 1987; Nowak and Lee 2013a) or may simply be a sign of the ecological flexibility of guerezas in plantation habitat and their ability to rely intensively on non-native food items (Fashing et al. 2012; Nowak and Lee 2013b; Eppley et al. 2015, 2017; Galán-Acedo et al. 2019b; Tesfaye et al. 2021).

All things considered, increased anthropogenic disturbance can reduce available patch size and increase resource competition, potentially leading to negative changes in primate abundance (Anderson et al. 2007; Chapman et al. 2013). In fact, many local elders around WWNSF mentioned that they had subjectively noticed a declining guereza population trend in the area, which they believe is due to the high level of anthropogenic disturbance—including habitat degradation, livestock grazing, human settlement, and agricultural expansion—over several decades (D. Yazezew pers. comm.).

The number of juvenile and infant individuals we recorded did not vary across the survey periods. This pattern suggests that reproduction within this guereza population occurs throughout the year, as has been documented at other guereza study sites in East Africa (Oates 1977b; Fashing 2002). The adult sex ratio recorded in WWNSF was quite even. Overall, understanding the sex ratio and age distribution of a species is imperative for effectively evaluating their population viability (Wilson et al. 1996). The small number of both infants and juveniles relative to adults in all habitat types in our study is cause for conservation concern (Struhsaker 2008), suggesting poor reproductive output and juvenile recruitment throughout WWNSF.

Lastly, Omo River guerezas were most abundant in the dry evergreen Afromontane forest ecosystem (i.e., the montane forest belt) between 2510 and 3100 m asl (Fig. 2). Common trees in this zone include *Olea europaea* ssp. *cuspidata* (Oleaceae), *Juniperus procera* (Cupressaceae), *Vernonia leopoldi* (Asteraceae), *Podocarpus falcatus* (Podocarpaceae), *Allophylus abyssinicus* (Sapindaceae), *Halleria lucida* (Stilbaceae), *Maesa lanceolata* (Primulaceae), *Ilex*

mitis (Aquifoliaceae), and *Olinia rochetiana* (Oliniaceae) (Ayalew 2018). Guerezas at WWNSF mostly avoid the higher Afroalpine habitat (above 3100 m), probably due to the restricted plant growth and dearth of suitable food resources at high elevations. This cold altitudinal zone includes few trees, extensive patches of the endemic forb *Kniphofia foliosa* (Asphodelaceae), shrub *Helichrysum* spp. (Asteraceae), and grass *Festuca* spp. (Poaceae) (Ayalew 2018), and is more energy-demanding for primates and other mammals than warmer lower altitudinal zones (Iwamoto and Dunbar 1983).

Conclusion

Because there have been no prior long-term population studies focused on Omo River guerezas, our study offers valuable baseline information with which to gauge future population density estimates and habitat use in their range. It is our hope that this study will be a catalyst for generating conservation-focused studies of primate species endemic to Ethiopia, and for using data-driven research to help guide forest and fauna management decisions within protected and non-protected sites. This should include directives to increase law enforcement measures, particularly forest patrols, through enhanced training and competency. Altogether, these initiatives could identify specific sites and/or habitat types known to harbor high guereza and other primate population densities, so that conservation actions may be more effective and efficient.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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