Home range, habitat use, and activity patterns of African wolves (*Canis lupaster*) in the Ethiopian highlands

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ABSTRACT

African wolves (*Canis lupaster*) and Ethiopian wolves (*C. simensis*) occur often sympatrically across habitats in the Ethiopian Highlands, with recent studies finding evidence for interspecific competition. However, unlike the well-studied Ethiopian wolf, comparatively little is known about the ecology of the African wolf in the Ethiopian Highlands. To address this empirical gap, we collected data on home range size, habitat use, and activity patterns of radio-collared African wolves at the Guassa Menz Community Conservation Area (GCCA) and Borena Saynt Worehimenu National Park (BSNP). We followed the African wolves (5 in GCCA, 6 in BSNP) for 16 months and had 659 ± 83 encounters with each individual. The mean 95% kernel density estimate home range size of African wolves was higher in BSNP (4.5 ± 1.5 km^2) than at GCCA (2.2 ± 0.7 km^2). In 55% (n = 3934) of the encounters the wolves were found to be solitary, whereas in other encounters we found them in groups of two to seven. At both sites, the African wolves were more often found in areas close to human settlements than in more intact habitat, and they were mainly active at dawn and dusk. These results show flexibility in African wolf socioecology in response to habitat fragmentation and anthropogenic disturbance. We recommend further studies on major causes of spatial and temporal niche partitioning of Ethiopian wolves and African wolves in the Ethiopian Highlands.

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1. Introduction

The African wolf *Canis lupaster* (AW) occurs in large parts of northern and eastern Africa, including Ethiopia (Rueness et al., 2011; Gaubert et al., 2012;). In the Afro-alpine biome of the Ethiopian highlands, AWs live sympatrically with the endangered Ethiopian wolf (EW) *Canis simensis* (Atickem et al., 2017; Gutema et al., 2018a). In contrast to the well-studied EW, little information on the behaviour, ecology, and conservation status of AWs in Ethiopia is available. In-depth research on the AW has been neglected in part because it was long considered a subspecies of the widely distributed and well-studied Eurasian golden jackal (*Canis aureus;* Rueness et al., 2011; Gopalakrishnan et al., 2018), and the behavioural ecology of the African wolf and the Eurasian golden jackal have not been reviewed independently of each other (Viranta et al., 2017). The taxonomy of the African wolf is also debated (Gippoliti, 2020), but here we follow Viranta et al. (2017) and Alvares et al. (2019) and regard it as Canis lupaster Hemprich and Ehrenberg, 1832.

In a previous study, we investigated the foraging ecology of AWs at two broadly similar sites in the Ethiopian Highlands, Guassa Menz Community Conservation Area (GCCA) and Borena-Saynt National Park (BSNP) (Gutema et al., 2019), focusing on the potential for interspecific competition between AWs and EWs in GCCA (Gutema et al., 2018a). Interactions between the two-canid species are typically agonistic and are determined by home-range advantage (the owner of the fighting place) and numerical superiority (Gutema et al., 2018a). AWs also tend to consume more diverse diets and occupy more anthropogenically-modified habitats than EWs, which are rodent specialists and prefer more intact habitats (Ashenafi et al., 2005; Gutema et al., 2018a; Marino, 2003; Marino et al., 2010).

Here we expand our ecological research on AWs by determining home-range size, habitat use, and activity patterns at GCCA and BSNP. Both areas consist largely of Afro-alpine grassland bordered by farmland. In a previous study, Admasu et al. (2004) estimated home range sizes of adult AWs (n = 3) in and adjacent to the Bale Mountains National Park (BMNP) in the southern Ethiopian Highlands. However, to provide a more complete insight into AWs home range and activity pattern, further research on spatial and temporal habitat use in areas with different anthropogenic impacts and EWs population is needed.

Home range size, habitat use and activity pattern are important parameters in conservation planning and can vary across different geographies (Mattisson et al., 2013). This is because of factors such as physiological adaptations, habitat quality, habitat size, weather, and the presence or absence of other species of canids (Kolenosky and Johnston, 1967; Kingdon (1977).

Creel (2002); Loveridge and Macdonald (2002)). According to Admasu et al. (2004), home ranges of AWs in BMNP varied between 8 and 48 km^2 (100% minimum convex polygon) and did not overlap with home ranges of EWs. In other parts of Africa, home ranges sizes vary from 1.1 to 20 km^2, depending on the distribution and abundance of food resources (Van Lawick and Van Lawick-Goodall, 1970; Kingdon, 1977; Poche et al., 1987; Fuller et al., 1989). On the other hand, in the areas where AWs are sympatric with black-backed (*Lupulella mesomelas*) and side-striped jackals (*L. adusta*), AWs uses dry open grassland (Kingdon, 1977) while *L. mesomelas* uses open woodland (Fuller et al., 1989), and *L. adusta* uses more densely vegetated habitats (Kingdon, 1977; Fuller et al., 1989). Activity patterns of canids can also vary across different ecologies. For instance, wolves were nocturnal in Italy (Ciucci et al., 1997); nocturnal with a tendency to bimodal activity in Spain (Vila` et al., 1995); active throughout day and night in Ontario, Canada (Kolenosky and Johnston, 1967). Furthermore, where they are sympatric, the peak activity time for AWs was during the day, while *L. adusta* was more active during the night and *L. mesomelas* at dawn (Fuller et al., 1989), which suggests co-existence mechanism between the species through niche partitioning. The studies indicate that the impacts of different factors can be observed on the canid species' home-range size (Admasu et al., 2004), activity pattern (Fedriani et al., 2001), and habitat use (Admasu et al., 2004, Pascale et al., 2004).

Ethiopian wolves' habitat use, home range, and activity pattern is well-documented (Ashenafi et al., 2005) in all its range. However, there is a lack of information regarding the AW ecology, in the central and northern parts of the Ethiopian landscape, where there is more habitat disturbance and less density of Ethiopian wolves. With our study, we aim to provide more data from two
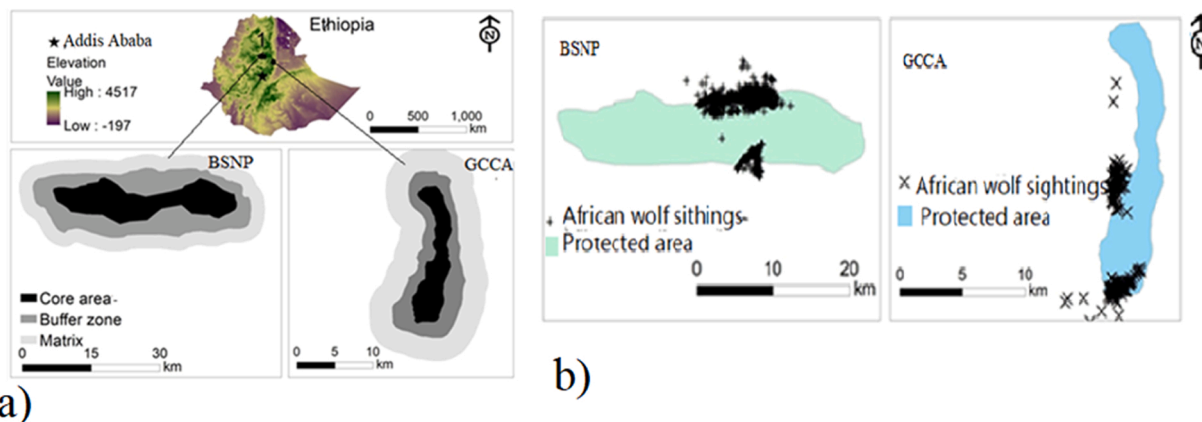

Fig. 1. a) Geographic position of the study areas in the Ethiopian Highlands, and Sketches of the proportion of the three zones at each of the study areas: core zone, where human and livestock activities are prohibited), buffer zone, where controlled livestock grazing is permitted, and matrix zone, which consists mainly of farmland and settlements,.

protected areas in the central and northern highlands of Ethiopia on home-range size, habitat use, and activity pattern of AWs. The study is important for further conservation of the endangered EWs and finding coexistence mechanisms of the two species.

2. Methods

2.1. Study area

We conducted the study in two protected areas in the highlands of central Ethiopia (Fig. 1), in the Guassa Menz Community Conservation Area (GCCA) and the Borena Saynt Worehimenu National Park (BSNP). The GCCA covers an area of 78 km² and consists mainly of Afro-alpine grassland and *Erica* moorlands. GCCA has been protected and managed by the local community for at least the last 400 years (Ashenafi et al., 2005). We focused our study on the southern part of the GCCA where AWs and EWs are sympatric and agonistic interactions between the species are common (Gutema et al., 2018a). The BSNP was established in 2001 and comprises 153 km² at elevations from 3200 to 4280 m (Eshete et al., 2018). Generally, both canid species are also sympatric in this protected area. However, here we studied AWs in the western part of the park, an area where we rarely observed EWs and where interference among the two species was almost absent.

The climate is similar in the two study areas, with a wet season extending from June to November and a dry season from December to May (Ashenafi et al., 2005; Venkataraman et al., 2015; Gutema et al., 2018b). Detailed climatic data are available only for GCCA where rainfall averages 1650 ± 243 mm per year, the average monthly temperature is $11.0 \pm 1.2\,°C$, and mean monthly low and high temperatures are $4.3 \pm 0.5\,°C$ and $17.8 \pm 0.3\,°C$, respectively (n = 6 years) (Fashing et al., 2014).

Both study sites are home to several mammal species endemic to Ethiopia. Besides EWs these are geladas (*Theropithecus gelada*), and Starck's hare (*Lepus starcki*). *Lophuromys*, *Crocidura*, *Arvicanthis*, and *Stenocephalemys* spp. are among the small mammals recorded in both areas (Gutema, 2019). *Lophuromys* are the most abundant small mammals in both GCCA (52%, relative abundance) and BSNP (54% relative abundance) (Chane and Yirga, 2014; Eshete et al., 2018; Gutema et al., 2018a). Both study sites are surrounded by villages. People grow barley and keep sheep and goats, providing similar anthropogenic food sources for the AWs (Gutema et al., 2019). Compared to BSNP (153 km2), GCCA is smaller (78 km2), and more disturbed (Gutema et al., 2019).

In much of the Ethiopian highlands, livestock grazing is the dominant land use practice of the local human communities (Zeleke and Hurni, 2001). Based on the level of disturbance, we delineated each study area into three zones. These are (1) the core zone, where all human and livestock activities are prohibited, (2) the buffer zone, where controlled livestock grazing is permitted, and adjacent to the protected area that is used only for livestock grazing), and (3) the matrix, the human-dominated areas adjacent to the protected area consisting mostly of farmland and settlements (Gutema et al., 2018a; Fig. 1).

b) Distribution of fixes of African wolves in the two study areas: Borena Saynt Worehimenu National Park (BSNP) and Guassa Menz Community Conservation Area (GCCA).

2.2. Trapping and collaring

Fourteen AWs (seven in GCCA and seven in BSNP) from eight packs (four packs from each site) were captured using rubber padded leg hold traps and fitted with very high frequency (VHF) collars. However, we tracked successfully only 11 AWs individual, 5 in GCCA, 6 in BSNP, (for detailed procedures of the capture and collaring see Gutema et al., 2018b).

2.3. Data collection

2.3.1. Spatial data

During 2016 and 2017, we collected spatial data of all 14 AWs. We recorded their positions of at 30 min intervals from distances of 50–150 m. We excluded three of the 14 wolves from the analyses, due to the low number of recorded locations. Two were found dead, possibly killed by humans, and for the third, the signal got lost after only three months (Gutema et al., 2018a). Our analyses are therefore based on 11 wolves (six in BSNP and five in GCCA).

When visual contact was not possible (particularly at night to minimize disturbance), tracking accuracy was determined by hiding a transmitter (collar) in an undisclosed position, enabling comparison between actual and estimated positions (Loveridge and Macdonald, 2002). Each collared AW individual was tracked 3–4 days in a month, as a focal, for 16 months.

2.3.2. Activity and habitat use

Focal observations were carried out on 11 AWs. During focal follows, to see the most habitat type used by AWs, habitat type (bushland, grassland, farmland, and woodland) were recorded. Similarly to see social organization of AWs, group size were also recorded at 30 min intervals if possible. The number of individual AWs in each pack (group size) was determined during tracking.

2.3.3. Data analysis

2.3.3.1. Home range estimates.
We estimated home range sizes for each individual using the minimum convex polygon (MCP) and fixed kernel density estimation (KDE) techniques. 100% MCP and 95% KDE home range sizes as well as 50% KDE core area sizes were used for each collared individual at each site. Although MCP has been widely criticized in that it often overestimates home range size

(Worton, 1989), we used present respective home range sizes to enable comparison with most previous studies (Admasu et al., 2004). We estimated home range sizes also by using KDE, which is generally regarded as better estimator of home range size than MCP (Wauters et al., 2007).

We then compared the home range sizes of the individuals at each site using linear models for the 95% and 50% KDE separately. Site was a fixed effect with two levels (i.e. BSNP and GCCA), considering each individual as the sampling unit, and home range size as the response variable.

2.3.3.2. Habitat use. Patterns of habitat use were determined from the nocturnal and diurnal locations where AWs were recorded during our study. Habitat use was assessed by categorizing the habitat type within a 20–100 m radius (based on the difference in landscape) around the focal animal's position. Variation in radius size was based on the type of habitat (e.g. in woodland, we used a smaller radius than in grassland where we can see the wolves from a distance). Habitats were defined as 'woodland' (>50% large trees), 'bushland' (>50% shrubs), 'open grassland' (>50% open land covered in grass and rocks, including such areas used for grazing), and agriculture (>50% crops, predominantly barley).

We compared habitat preferences using general linear models for each site separately. In this model, habitat type with four levels (farmland, grassland, bushland, and woodland) and daytime with two levels (day and night) were used as fixed effect factors and individual collared animals as random effects.

2.3.3.3. Activities and group size. Activities of the focal wolf were recorded as 'travelling' (moving without hunting or feeding), 'resting' (sleeping, sitting), 'hunting' (attempting to capture prey), 'feeding' (ingesting food) and 'social interaction' (playing, greeting, grooming, group howling). To determine activity peaks, we divided activities into two categories inactive (resting) and active (all other behaviours). For this analysis, the 24-hour period was divided into four six-hour periods, 04:01–10:00 h (dawn-morning), 10:01–16:00 h (midday), 16:01–22:00 h (dusk-evening), 22:01–04:00 h (midnight). The number of conspecifics nearby was also recorded. We considered animals to be in a group when they were < 50 m from one another.

We estimated the percentage of time spent per hour in relation to activity with two levels (active and resting) and time (i.e. 24-hours cycle) using a general linear model. All analyses were carried out in R version 3.5.1 (R Core Team, 2018).

3. Results

3.1. Home range

We recorded 7224 AW locations (BSNP: n = 4032; GCCA: n = 3193) between April 2016 and November 2017 (for details on each individual see Table S1). The mean $\pm$ SD 95% KDE home range size of AWs was twice as high (4.5 $\pm$1.5 km^2) at BSNP and then at GCCA (2.2 $\pm$0.7 km^2) (Table 1; Fig. 2). The 50% KDE the core area sizes were also higher at BSNP (0.59 $\pm$0.17) km^2) than at GCCA (0.38 $\pm$0.10). Similarly, the mean $\pm$ SD 100%MCP were 8.4$\pm$ 3.1 in GCCA and 13 + 4.6 in BSNP. Home range and core area size (km^2) varied significantly between the two sites, 95% (t = 10.12, df = 9, P = 0.01) and 50% KDE (t = 6.614, df = 9, P = 0.03; Table S2; Table TS3).

3.2. Habitat use

Patterns of habitat use were inferred from 3919 diurnals and 3302 nocturnal locations recorded for the AWs in our study. At both BSNP and GCCA, AWs were mainly observed in the matrix and buffer zones of the protected areas, and only rarely in the core zones. In BSNP (of 4076 observation), 51% of AW sightings were in the matrix, 43% in the buffer, and 6% in the core. Conversely, in GCCA (of 3170 observation), 57% of AW sightings were in the buffer, 41% in the matrix, and 2% in the core.

Table 1

Home range size of African wolves at two study sites, Borena Saynt National Park (BSNP) and Guass Menz Community Conservation Area (GCCA). Home ranges sizes and core area sizes (km^2) were estimated using the 100% minimum convex polygon (MCP) and 95% and 50% fixed kernel density estimation (KDE) techniques.

| Site	ID	age	sex	# of days Tracked	# of fixes	100% MCP	95% KDE	50% KDE
BSNP	Anm350	adult	female	49	787	10.7	3.17	0.49
	Anm370	adult	male	47	816	6.63	2.26	0.52
	Anm390	adult	male	48	643	15.40	5.75	0.68
	Anm470	adult	Female	48	661	19.77	4.76	0.73
	Anm430	subadult	male	50	545	12.57	5.70	0.35
	Anm510	subadult	female	49	623	16.01	5.33	0.78
GCCA	Anm290	adult	male	51	656	12.39	2.68	0.35
	Anm310	adult	male	50	564	5.17	2.64	0.46
	Anm450	subadult	female	49	676	9.16	1.46	0.27
	Anm490	adult	female	48	603	5.31	2.85	0.49
	Anm550	adult	female	50	670	9.73	1.58	0.31
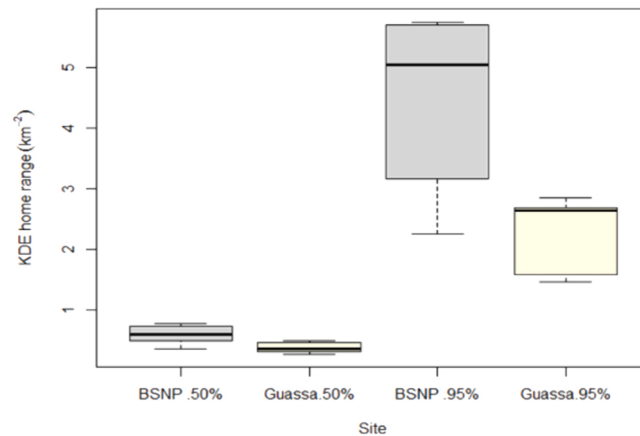
Fig. 2. Comparison of mean ± SD 95% and 50% kernel density estimate (KDE) home range sizes (km^2) of African wolves in Borena Saynt National Park (BSNP, grey boxes, n = 6) and Guassa Menz Community Conservation Area (GCCA, yellow boxes, n = 5).

At both sites, bushland was the habitat type used most by AWs during the day, while farmland and open grassland were the most used at night in both sites (Fig. 3; Table S2).

3.3. Activities and group size

Frequency of occurrence of each activity type varied across time at both sites (Fig. 4). Although AWs were active during both day and night, their activity peaks were between 04:00 and 10:00 (dawn-morning) and 16:00–20:00 (dusk-evening) (Fig. 4). In BSNP, AWs spent 41.0% of their time travelling, 25.0% hunting, 16.2% resting, and 15.6% feeding, while in GCCA, they spent 27% of their time resting, 25% travelling, 24% hunting, and 19.5% feeding (Table S4).

AWs were solitary in 55% of total sightings (n = 3934) and groups of 2–7 during the other 45% (n = 3291) (Table S4). AWs were usually observed alone during the daytime and in groups at night (Fig. 5). AWs were more often found in groups at GCCA than at BSNP (Table S4; Table S5). In particular, of diurnal AW sightings (All records of AWs during day time, in this study), 42% at GCCA (n = 2222) were of groups ($\geq$2 individuals) versus 27% at BSNP (n = 1707). During the night, 67% of AW sightings at GCCA (n = 1663) were of groups versus only 30% at BSNP (n = 1707). These differences in grouping patterns between sites were significantly different (t = 25.9, df=1, p = 0.001).

4. Discussion

This study addressed the ranging, habitat use, and activity patterns of AWs at two sites in the Ethiopian Highlands.
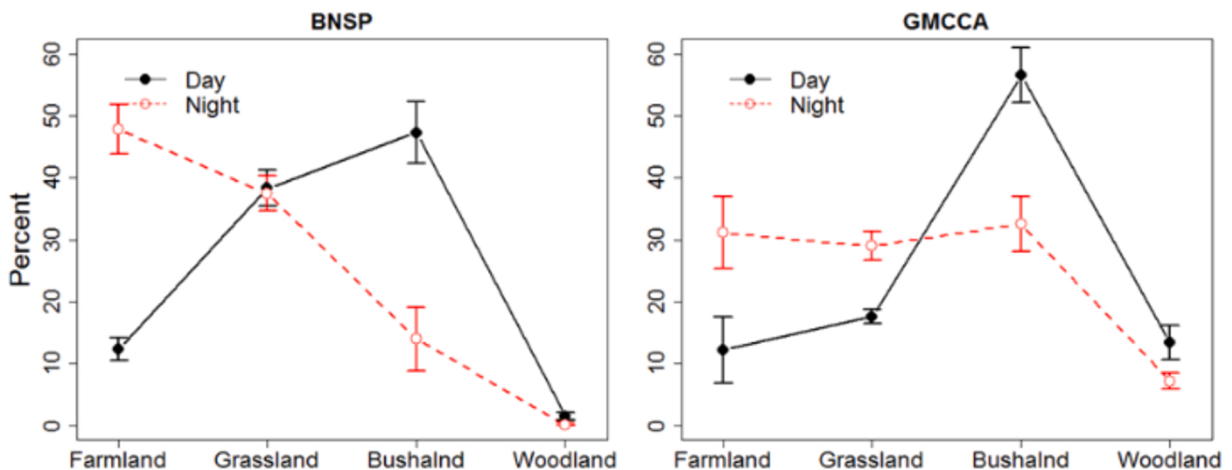

Fig. 3. Mean percentage time spent by African wolves in different habitat types during the day and night at each study site, Borena Saynt National Park (BSNP), Guassa Menz Community Conservation Area (GCCA).
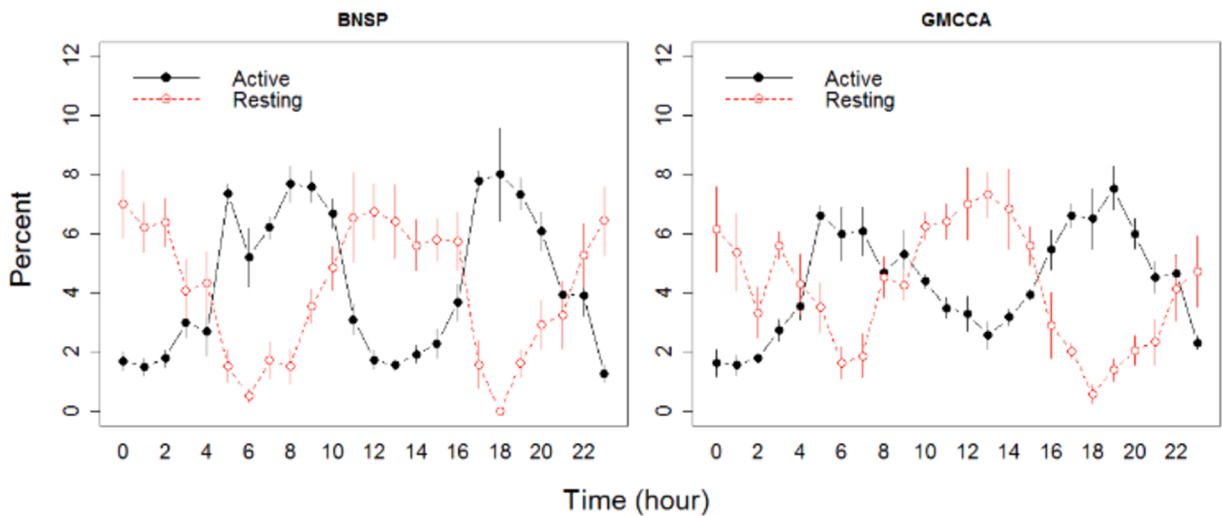
Fig. 4. Percentage of active time (travelling, feeding, and social interaction) during one-hour time intervals based on direct observations of 11 collared African wolves in Borena Saynt National Park (BSNP, n = 6) and Guassa Menz Community Conservation Area (GCCA, n = 5).
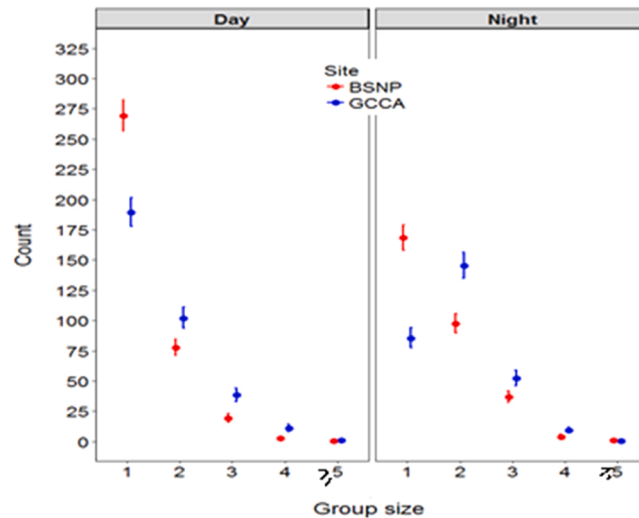

Fig. 5. Total counts of African wolf individuals that were recorded during focal follows of 11 collared African wolves at BSNP (n = 6) and GCCA (n = 5). Here group size means, the number of individual African wolves observed in a group.

4.1. Home range

The study shows that the home range size of AWs varies across the study sites, in that the home range size of AW populations in BSNP was more than twice that of the populations in GCCA (4.5 versus 2.2 km^2 95% KDE). This might be a result of differences in disturbances, and the presence of competition with EWs at GCCA. GCCA is a community conservation area, where the community uses some resources in the protected area with the controlled system (eg., collecting grasses once a year including from the core area), which might disturb wildlife species' behaviour in the area. On the other hand, BSNP is a governmental national park, where relatively both the buffer and core areas are restricted from human activities. This disturbance difference between the two sites might be among the major factors for the home range size difference. The second factor for the AWs homerange difference in this study might be due to the serious interference competition with EWs. In our former study, we confirmed that AWs were chased by EWs from the core zone and restricted to the buffer zone in GCCA (Gutema etal., 2018), while in BSNP relatively AWs used the core zone of the protected area.

Though sex and age are among the factors that affect home range size, in this study the proportion of sex and age of the collared AWs between the two sites were almost the same (Gutema et al., 2019). However, a further detailed study is needed to evaluate the major factors that affect homerange size of AWs by increasing number of collared AWs, study sites and other possible factor (Erlinge et al., 1990; Mysterud et al., 2001; Caro and Stoner, 2003; Hayes et al., 2007; Ofstad et al., 2016).

4.2. Habitat use

In both study areas, AWs are known to prefer areas in proximity to human habitats (Gutema et al., 2018, 2019). This might be explained by the lower rodent hunting efficiency of AWs in Afro alpine habitat compared to EWs (Gutema et al., 2019) and the availability of anthropogenic resources (such as livestock carcasses and waste disposal area) around human settlement. However, relatively more AWs were recorded in the core zone in BSNP (6% of the total locations recorded, n = 4076) compared to the core zone of GCCA (2%, n = 3170). While this is a minor difference, it could be due to the presence of EWs in the core areas of GCCA (Gutema et al., 2019). Admasu et al. (2004), from the study of seven collared AWs in and adjacent to BMNP, found that AWs were restricted to the mosaic of farmland, grassland, and woodland of the edge and adjacent to the Park and do not overlap with EWs. This might be explained by the dominance of EWs due to their high population in the park (estimated total population= 250 individuals; Marino and Sillero-Zubiri, 2011).

Bushland is the habitat most used by AWs during the daytime, while farmland and open grassland are more commonly occupied at night. The bushland, consisting of structurally diverse shrubs, offers cover and protection from anthropogenic pressure (Admasu et al., 2004; Šálek et al., 2014). Similarly, in highlands of BMNP, the majority of diurnal resting sites were recorded in the bush (Admasu et al., 2004), while in Serengeti, the golden jackal was most common on grassland habitats during the day (Moehlman, 1986).

On the other hand, in this study, woodland habitats were not often used by AWs. This might be due to the predators in the woodland, because during the study period, the presence of leopards (*Panthera pardus*) was confirmed. In previous studies, consumption or killing of jackals by leopards was reported in Africa (Loveridge and Nel, 2004; Hayward, Henschel et al., 2006).

4.3. Activity pattern and group size

Our study shows that AWs are mainly crepuscular (active at dawn and dusk) but they were also active both during the day and at night in both study sites. This is similar to the behaviours of black-backed jackals in South Africa, where they forage mostly during the early morning and late afternoon (Kaunda, 2001). On the other hand, the sympatric EW is active mainly during the day (diurnal) due to its primary diet, subterranean diurnal rodents (Sillero-Zubiri and Gottelli, 1995; Ashenafi et al., 2005; Sillero-Zubiri et al., 2004; Eshete et al., 2018). Thus, Aws and EWs may reduce direct interspecific competition by exploiting the same area at a different time of day. The AWs in GCCA spent a higher proportion of time resting (27%, n = 2979) than the AWs in BSNP (16%, n = 4035). This might be due to the interference competition with EWs that exclude them from using intact habitat during daytime, and from being active in areas close to human settlement in the buffer zone during daytime (Machado et al., 2017).

Large group size of AWs was recorded in GCCA. This might be the mechanism of defending EWs, as the interference competition is more severe in this site (Gutema etal., 2018). This is common in other species of canids, for instance, wild dogs manage to co-exist with spotted hyenas due to their large group sizes that help them to adequately defend their kills (Darnell et al., 2014).

5. Conclusion

The study revealed the AW's flexibility in home range size that shows the ability to respond to habitat fragmentation or anthropogenic impacts. In addition, the results indicate niche partitioning between the AWs and the endangered EWs (that means they prefer different habitat type and activity time) which might be among the factors for the coexistence of the two species in all EW range. However, with current trends in human population growth in the Ethiopian highlands (Tolessa et al., 2017), anthropogenic impacts may tend to give AWs a competitive dominance over EWs, particularly in the fragmented habitats where AWs might use the intact habitat for protection from human attack. Hence, the results support the emerging picture of AWs as ecological generalists who will proliferate at the expense of EWs if intact habitat (Afroalpine) is not protected. From our result, we recommend further studies on detailed factors that affect the spatial ecology of AWs in the Ethiopian Highlands, by increasing the sample size of the study individuals and site. This contribute for conservation of the endangered EWs, enhancing coexistence of the two wolf species.

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 that has been used is confidential.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02324.

References

Admasu, E., Thirgood, S.J., Bekele, A., Laurenson, M.K., 2004. Spatial ecology of golden jackal in farmland in the Ethiopian Highlands. Afr. J. Ecol. 42, 144–152.

Alvares, F., Bogdanowicz, W., Campbell, L.A.D., Godinho, R., Hatlauf, J., Jhala, Y., Kitchener, A., Koepfli, K.P., Krofel, M., Moehlman, P.D., Senn, H., Sillero-Zubiri, C., Viranta, S., Werhahn, G., 2019. Old World Canis spp. with taxonomic ambiguity: Workshop conclusions and recommendations. Cibio. Vairão, Port. 2019.

Ashenafi, Z.T., Coulson, T., Sillero-Zubiri, C., Leader-Williams, N., 2005. Behaviour and ecology of the Ethiopian wolf (Canis simensis) in a human-dominated landscape outside protected areas. Anim. Conserv. 8 (2), 113–121.

Atickem, A., Simeneh, G., Bekele, A., Mekonnen, T., Sillero-Zubiri, C., Hill, R.A., Stenseth, N.C., 2017. African wolf diet, predation on livestock and conflict in the Guassa Mountains of Ethiopia. Afr. J. Ecol. 55 (4), 632–639. https://doi.org/10.1111/aje.12399.

Caro, T.M., Stoner, C.J., 2003. The potential for interspecific competition among African carnivores. Biol. Conserv. 110 (1), 67–75.

Chane, M., Yirga, S., 2014. Distribution and diversity of small mammals in Borena-Sayint National Park, South Wollo, Ethiopia: Implications of habitat specialization. Int. J. Biodivers. Conserv. 6 (5), 415–421.

Creel, S., Creel, N.M., 2002. The African wild dog: behavior. ecology, and conservation. Princeton University Press.

Darnell, A.M., Graf, J.A., Somers, M.J., Slotow, R., Szykman Gunther, M., 2014. Space use of African wild dogs in relation to other large carnivores. PloS One 9 (6), e98846.

Eshete, G., Sillero-Zubiri, C., Cieraad, E., Musters, C.J.M., De Snoo, G.R., De Iongh, H.H., Marino, J., 2018. Does livestock predation reflect in negative local perceptions of Ethiopian wolves in South Wollo. Int. Soc. Trop. Ecol. 59 (1), 11–19.

Fuller, T.K., Biknevicius, A.R., Kat, P.W., Valkenburgh, B.V., Wayne, R.K., 1989. The ecology of three sympatric jackal species in the Rift Valley of Kenya. Afr. J. Ecol. 27 (4), 313–323.

Gaubert, P., Bloch, C., Benyaoub, S., Abdelhamid, A., Pagani, P., Djagoun, C.A.M.S., Couloux, A., Dufour, S., 2012. Reviving the African wolf Canis lupus lupaster in North and West Africa: a mitochondrial lineage ranging more than 6,000 km wide. PLoS ONE 7 (8), e42740.

Gippoliti, S., 2020. Records of Ethiopian and Eritrean mammals in Italian literature and museums, with some taxonomic notes. Biogeogr. – J. Integr. Biogeogr. 35, 17–32.

Gopalakrishnan, S., Sinding, M.H.S., Ramos-Madrigal, J., Niemann, J., Samaniego Castruita, J.A., Vieira, F.G., Carøe, C., Montero, M. d M., Kuderna, L., Serres, A., González-Basallote, V.M., Liu, Y.H., Wang, G.D., Marques-Bonet, T., Mirarab, S., Fernandes, C., Gaubert, P., Koepfli, K.P., Budd, J., Rueness, E.K., Heide-Jørgensen, M.P., Petersen, B., Sicheritz-Ponten, T., Bachmann, L., Wiig, Ø., Hansen, A., Gilbert, M.T.P., 2018. Interspecific gene flow shaped the evolution of the genus Canis. Curr. Biol. 28 (21), 3441–3449 e3445.

Gutema, T.M., Atickem, A., Bekele, A., Sillero-Zubiri, C., Kasso, M., Tsegaye, D., Venkataraman, V.V., Fashing, P.J., Zinner, D., Stenseth, N.C., 2018a. Competition between sympatric wolf taxa: an example involving African and Ethiopian wolves. R. Soc. Open Sci. 5 (5), 172207.

Gutema, T.M., Atickem, A., Lemma, A., Bekele, A., Sillero-Zubiri, C., Zinner, D., Farstad, W.K., Arnemo, J.M., Stenseth, N.C., 2018b. Capture and immobilization of African wolves (Canis lupaster) in the Ethiopian Highlands. J. Wildl. Dis. 54 (1), 175–179.

Gutema, T.M., Atickem, A., Tsegaye, D., Bekele, A., Sillero-Zubiri, C., Marino, J., Kasso, M., Venkataraman, V.V., Fashing, P.J., Stenseth, N.C., 2019. Foraging ecology of African wolves (Canis lupaster) and its implications for the conservation of Ethiopian wolves (Canis simensis). R. Soc. Open Sci. 6 (9), 190772.

Hayes, L.D., Chesh, A.S., Ebensperger, L.A., 2007. Ecological predictors of range areas and use of burrow systems in the diurnal rodent, Octodon degus. Ethology 113 (2), 155–165.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., Kerley, G.I.H., 2006. Prey preferences of the leopard (Panthera pardus). J. Zool. 270, 298–313.

Kaunda, S., 2001. Spatial utilization by black-backed jackals in southeastern Botswana. Afr. Zool. 36 (2), 143-125.

Kingdon, J., 1977. East African mammals. An atlas of evolution in. Africa (Carnivores). Academic Press,, New York.

Loveridge, A.J., Macdonald, D.W., 2002. Habitat ecology of two sympatric species of jackals in Zimbabwe. J. Mammal. 83 (2), 599–607.

Loveridge, A.J., Nel, J.A., 2004. Black-backed jackal. In: SilleroZubiri, C., Hoffmann, M., Macdonald, D.W. (Eds.), Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan. IUCN-SSC Canid Specialist Group, Cambridge, UK, pp. 161–166.

Machado, R.F., Cerezer, F.O., Hendges, C.D., Cáceres, N.C., 2017. Factors affecting the home range size of felids (Mammalia, Carnivora) with emphasis on three American species. Ecol. Austral 27 (2), 232–241.

Marino, J., 2003. Threatened Ethiopian wolves persist in small isolated Afroalpine enclaves. Oryx 37 (1), 62–71.

Marino, J., and Sillero-Zubiri, C. 2011. Canis simensis. The IUCN RedList of Threatened Species 2011, e.T3748A10051312. (doi: 10.2305/IUCN.UK. 2011–1.RLTS. T3748A10051312.en).

Marino, J., Mitchel, R., Johnson, P.J., 2010. Dietary specialization and climatic-linked variations in extant populations of Ethiopian wolves. Afr. J. Ecol. 48 (2), 517–525.

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D., Rauset, G.R., Pedersen, H.C., 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. Oecologia 173 (3), 813–825.

Moehlman, P.D., 1986. Social organization in jackals: the complex social system of jackals allows the successful rearing of very dependent young. Am. Sci. 75 (4), 366–375.

Mysterud, A., Pérez-Barbería, F.J., Gordon, I.J., 2001. The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. Oecologia 127, 30–39.

Ofstad, E.G., Herfindal, I., Solberg, E.J., Sæther, B.E., 2016. Home ranges, habitat and bodymass: simple correlates of home range size in ungulates. Proc. R. Soc. B: Biol. Sci. 283 (1845), 20161234.

R Core Team 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rueness, E.K., Asmyhr, M.G., Sillero-Zubiri, C., Macdonald, D.W., Bekele, A., Atickem, A., Stenseth, N.C., 2011. The cryptic African wolf: Canis aureus lupaster is not a golden jackal and is not endemic to Egypt. In: PLoS ONE, 6.

Šálek, M., Červinka, J., Banea, O.C., Krofel, M., Ćirović, D., Selanec, I., Penezić, A., Grill, S., Riegert, J., 2014. Population densities and habitat use of the golden jackal (Canis aureus) in farmlands across the Balkan Peninsula. Eur. J. Wildl. Res. 60, 193–200.

Sillero-Zubiri, C., Gottelli, D., 1995. Diet and feeding behavior of Ethiopian wolves (Canis simensis). J. Mammal. 76 (2), 531–541.

Sillero-Zubiri, C., Hoffmann, M., Macdonald, D.W. (Eds.), 2004. Canids: foxes, wolves, jackals, and dogs: status survey and conservation action plan. IUCN, Gland, Switzerland.

Tolessa, T., Senbeta, F., Kidane, M., 2017. The impact of land use/land cover change on ecosystem services in the central highlands of Ethiopia. Ecosyst. Serv. 23, 47–54.

Venkataraman, V.V., Kerby, J.T., Nguyen, J.N., Ashenafi, Z.T., Fashing, P.J., 2015. Solitary Ethiopian wolves increase predation success on rodents when among grazing gelada monkey herds. J. Mammal. 96 (1), 129–137. https://doi.org/10.1093/jmammal/gyu013.

Viranta, S., Atickem, A., Lars, W., Stenseth, N.C., 2017. Rediscovering a forgotten canid species. BMC Zool. 2, 6. https://doi.org/10.1186/s40850-017-0015-0.

Wauters, L.A., Preatoni, D.G., Molinari, A., Tosi, G., 2007. Radio-tracking squirrels: performance of home range density and linkage estimators with small range and sample size. Ecol. Model. 202 (3–4), 333–344.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70, 164–168.

Zeleke, G., Hurni, H., 2001. Implications of land use and land cover dynamics for mountain resource degradation in the Northwestern Ethiopian highlands. Mt. Res. Dev. 21, 184–192.