Behavioral ecology of the African wolf (Canis lupaster) and its implication for

Ethiopian wolf (Canis simensis) conservation in the Ethiopian Highlands

Tariku Mekonnen Gutema

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Center for Ecological and Evolutionary Synthesis

Department of Biosciences

Faculty of Mathematics and Natural Sciences

University of Oslo

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Abstract

Recent rapid increases in human populations are leading to conversion of wildlife habitats into agricultural areas and human settlements. This is forcing wildlife populations to increasingly concentrate into confined protected areas, which in turn increases competition between wildlife species for limited space and food. African wolves (*Canis lupaster*) and Endangered Ethiopian wolves (*C. simensis*) are sympatric in parts of the Ethiopian Highlands. The Ethiopian wolf is an ecological specialist and only small populations remaining which makes it sensitive to both exploitative and interference competition from other carnivores. To better understand these dynamics this thesis focuses on the behavioral ecology of the African wolf and its impact on Ethiopian wolves and their conservation. Due to their perceived impact as predators on livestock, I also studied the extent of human-carnivore conflict.

The study was carried out from March 2015 to June 2017 in Guassa Menz Community Conservation Area and Borena Saynt Worehimenu National Park in the central Ethiopian Highlands. Focal watches of 14 colalred African wolves were carried out to study their spatial and foraging ecology, and habitat use. The wolves were captured using rubber-lined foothold traps, immobilized with dexmedetomidine-ketamine and fitted with very high frequency (VHF) collars. The nature of African wolf-Ethiopian wolf interactions was studied using a focal watch technique whenever two wolves came into contact. We used binomial logistic regression to analyse the outcome of agonistic interactions between the two species. The diet of African wolf was studied both from scan sampling of focal individuals and faecal analysis. The diet preference of African wolf was compared to the published diet of Ethiopian wolves. Individual home ranges of African wolves were estimated using minimum convex polygon (MCP) and fixed kernel density estimation (95% and 50% KDE) from the locations recorded from collared African wolves. We compared the abundance of rodent species in faeces in different habitat using the generalized linear model. Interviews and faecal analysis were used to evaluate the nature and extent of human-carnivore conflict. From 82 encounters observed between AWs and Ethiopian wolves, interactions between the two wolves were typically antagonistic, with Ethiopian wolves dominating in the core (undisturbed) habitat and AWs in the human-disturbed areas (Paper I). Direct observations and faecal analysis indicated that African wolves are opportunistic foragers, which feed on diverse food items, unlike the Ethiopian wolves that are more of a rodent specialist. These results suggest that interference competition with African wolves might be another potential threat to Ethiopian wolves while the exploitative competition between the two wolf species appears to be limited (Papers I, II). The study also investigated the importance of African wolves in rodent control and waste management through their removal of rodent and livestock carcasses near farm households in the Ethiopian Highlands (Paper II). In paper III we demonstrated the plasticity of African wolves in home range use, which indicates their ability to respond to human-induced landscape changes. African wolf's home range was estimated at 2.2 - 4.5 km² based on 95% KDE, and 5.2 - 19.8 km² 100% based on MCP analysis in different landscapes (Paper III). African wolves used bushland habitat during the day, and farmland and open grassland during the night when human presence was minimal. A frican wolves were the most important wild predator of livestock in the study area and consequently the community had negative attitude toward them; African wolves attracted 80.8% negative attitude compared to 14% for Ethiopian wolves (Paper IV).

Based in the results of this study we conclude:

- *1)* African wolves can be a potential threat to the endangered Ethiopian wolves through interference competition, while exploitative competition appears to be low,
- African wolves have an omnivorous diet with a prominent scavenging component, unlike the more strict rodent hunting specialist Ethiopian wolves,
- *3)* African wolves home range sizes are flexible based on landscape; African wolves prefer areas in proximity to human settlements while Ethiopian wolves prefer core zone, and
- 4) African wolves are involved on serious human-predator conflict, but they are also associated with an important ecosystem service role (as rodent pest control and envinmental cleaner)

List of papers

This thesis consists of four papers (three published articles and one manuscript) and one appendix, which are referred by the Roman numerals as follow:

- Paper I: Gutema, T. M., A. Atickem, A. Bekele, C. Sillero-Zubiri, M. Kasso, D. Tsegaye, V. V. Venkataraman, P. J. Fashing, D. Zinner, and N. C. Stenseth. 2018a. Competition between sympatric wolf taxa: an example involving African and Ethiopian wolves. *Royal Society Open Science* 5:172207.
- Paper II: Gutema, T. M., Atickem, A., Tsegaye, D., Bekele, A., Sillero-Zubiri, C., Marino, J., Kasso, M., Venkataraman, V. V., Fashing, P. J., and Stenseth, N. C. (2019). Ranging behaviour, habitat use and activity patterns of African wolves (*Canis lupaster*) in the Ethiopian highlands. *Royal Society Open Science*, 6:190772.
- Paper III: Gutema, T. M., A., Atickem, Tsegaye, Dessalegn Chala, A. Bekele, C. Sillero-Zubiri, D. Zinner, V. V. Venkataraman, P. J. Fashing & Stenseth, N. C. (2019). Ranging, habitat, and activity patterns of African wolf (*Canis lupaster*) in two landscapes of the Ethiopian Highlands. Manuscript
- Paper IV: Atickem, A., G. Simeneh, A. Bekele, *T. Mekonnen, C. Sillero-Zubiri, R. A. Hill, and N. C. Stenseth. 2017. African wolf diet, predation on livestock and conflict in the Guassa mountains of Ethiopia. *African Journal of Ecology* 55:632-639.

Appendix

Gutema, T. M., A. Atickem, A. Lemma, A. Bekele, C. Sillero-Zubiri, D. Zinner, W. K. Farstad, J. M. Arnemo, and N. C. Stenseth. 2018b. Capture and Immobilization of African wolf (*Canis lupaster*) in the Ethiopian Highlands. *Journal of Wildlife Diseases* 54:175-179.

*T. Mekonnen (first and second name) was used for this paper. Since 2018, for simplicity, I have started using third name (Gutema T. M) for all my scientific papers.

1. Introduction

1.1 History and distribution of the African wolf

The African wolf (Canis lupaster; henceforth AW; Fig. 1a) was hitherto a cryptic species, and has only recently been described (Rueness et al. 2011). For over a century, the AW was considered to be the widely distributed golden jackal (C. aureus; Bickford et al. 2007), and was only recently reclassified as a wolf due to their close phylogenetic relationship with the grey wolf (C. lupus). It was first discovered in the Ethiopian highlands (Rueness et al. 2011), and latter in northern Africa, from Egypt through the Sahara desert and into Senegal (Gaubert et al. 2012). These studies were based on mitochondrial DNA which is maternally inherited and represents only a short segment of the entire genome. Hence, true confirmation of the AW stan as a species remained uncertain until 2015 when the ful (Koepfli et al. 2015). Genome sequence showed it is in fact closely related to the grey wolf (Koepfli et al. 2015). After including several samples from many African countries, Viranta et al. (2019) suggested that the entire golden jackal population in Africa is indeed the AW, and that the golden jackal range excludes Africa, ranging from the Arabian Peninsula to Asia and Europe. The discovery of the AW reveals the importance of DNA sequencing for identifying cryptic species and the taxonomy of African mammals is still incomplete (Bickford et al. 2007). Some researchers named the AW as C. anthus (Koepfli et al. 2015), whereas others prefered C. lupaster (Rueness et al. 2011). In this thesis, we follow the recommendation of Viranta et al. (2017) and Alvares et al. (2019) and use Canis lupaster Hemprich and Ehrenberg 1832.

Since the AW in Ethiopia has long been erroneously considered the widely distributed golden jackal, there was not much interest in their behaviour and ecology. More information about the species is available from Kenya (Fuller et al. 1989) and northern Tanzania (Wyman 1967; van Lawick & Goodall 1970; Lamprecht 1978), which may probably represent a different subspecies than the wolves in northern Africa and Ethiopia.

AWs are found in large parts of northern and eastern Africa including the Ethiopian Highlands (Moehlman & Jhala 2013). The fossil record suggests that the AW evolved outside of Africa and

joined the other two species in East Africa within the last 500 000 years (Van Valkenburgh and Wayne 1994). Paleontological and molecular data suggest that the AW entered East Africa after the other two species had been present there for some time (Girman *et al.* 1993; Van Valkenburgh and Wayne 1994). A recent study revealed the AW descended from genetically admixture of 72% grey wolf and 28% Ethiopian wolf (*Canis simensis*; henceforth EW) ancestry (Shyam *et al.* 2018).

AWs typically occur in sympatry with at least one other mid-sized canid species, such as, black- backed jackal *Canis mesomelas*, side-striped jackal *C. adusta* or EWs (Fuller *et al.* 1989; Van Valkenburgh & Wayne 1994; Rueness *et al.* 2011). The AW and the two jackals are typical mesocarnivores (5-15 kg) mainly feeding on smaller prey such as invertebrates and rodents which they scavenge opportunistically (Temu *et al.* 2018). However, side-striped jackals are omnivorous scavengers, while black backed jackals and AWs are thought to be more predatory but still omnivorous (Nowak 1999).

1.2 Distribution and threats of Ethiopian wolves

The EW (Fig. 1b) is the rarest canid in the world and Africa's most threatened carnivore. It is endemic to the Ethiopian highlands (Marino and Sillero-Zubiri 2011), and found only in six isolated populations, with fewer than 500 adult individuals remaining under increasing threat of human interference, habitat degradation and disease (Marino 2003; EWCA 2011, 2017). Rabies and canine distemper virus (CDV) have posed the most immediate threat, responsible for past population crashes (Randall et al. 2006). Only during the last five years, the largest EW population in the Bale Mountains, which was around 300 individuals, declined by 30% due to rabies and CDV (Marino and Sillero-Zubiri 2011). EWs are an ecological specialist (Sillero-Zubiri 1994; Marino 2003; Ashenafi *et al.* 2005). The current range of EWs is limited to six isolated mountain ranges at altitudes of 3,000–4,500 m, including more than half remaining individuals in the Bale Mountains (Marino 2003, EWCA 2011). These are, roughly from North to South, Simien Mountains (Godnar), Abuna Yosef (North Wollo), Borena Saynt Worehimenu National Park (South Wollo), Guassa Community Conservation Area (Shoa), Arsi Mountains, and Bale Mountains; they have been recently extirpated from Mount Guna and Mount Choke (EWCA

2011). Molerats (*Tachyoryctes spp*) are the preferred diet of the EW, followed by grass rats (*Arvicanthis blicki*), and swamp rats (*Otomys typus*) (Morris and Malcolm 19777; Sillero-Zubiri and Gottelli 1996, Sillero-Zubiri et 1994; Marino 2003; Ashenafi *et al.* 2005; Yihune *et al.* 2008; Yihune and Bekele 2014).

Ecological specialist carnivores are sensitive to impacts of competition, which depend on their specific diets, habitats and activity patterns (Smith *et al.* 2018). This is because, unlike generalists, specialists have less ability to use the advantage of avoidance mechanisms for coexistence (Elmhagen *et al.* 2002; Grassel *et al.* 2015; Smith *et al.* 2018) which may lead to extinction (Elmhagen *et al.* 2002). For instance, African wild dog (*Lycaon pictus*) populations may have become locally extinct in parts of their range due to the presence of larger carnivores such as lions (*Panthera leo*) and spotted hyaenas *Crocuta crocuta* (Creel 2001).



Figure 1. African wolf (a: camera trap photo from Guassa Community Conservation Area) and Ethiopian wolf (b: Bale Mountains National Park, <u>www.ethiopianwolf.org</u>).

1.3 Competition among mammalian carnivores

Competition is one of the most important factors shaping the distribution and abundance of carnivore species (Caro and Stoner 2003). When carnivores share the same resources and the

supply of that resource is limited, interspecific competition is inevitable (Gatto 1990). Keddy (1989) defined interspecific competition as "the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability". Interspecific competition can occur in several forms including interference competition, exploitative competition and intraguild predation (Palomares and Caro 1999; Caro and Stoner 2003; Glen and Dickman 2005; Binfield 2008). Interference competition occurs when individuals are directly antagonistic toward others such that they exclude others from a contested resource (Glen and Dickman 2005) or steal prey or other food that was caught or collected by the other animal, kleptoparasitism (Gorman et al. 1998; Höner et al. 2002; Carbone et al. 2005). Exploitative competition occurs when one species is more efficient than its competitors at exploiting available resources (Case and Gilpin 1974). In a more extreme case, the subordinate species maybe killed by the dominant species, which is termed as intraguild predation, characteristics of both competition and predation (Polis and Holt 1992). Intraguild predation, killing and sometimes eating of potential competitors (Polis and Holt, 1992; Palomares & Caro 1999), might remove a source of mortality for the killer or its offspring (Eaton 1979) or free up food resources that would be consumed by the victim (Polis et al. 1992), or killers might accrue energetic benefits from consuming their victims (Palomares & Caro 1999).

The degree of competition between carnivore species depends on prey abundance, diversity of prey, the diet preferences and habitat availability of competing species (Bhattarai & Kindlmann 2012; Lovari *et al.* 2015; Simcharoen *et al.* 2018). Gese *et al.* (1996) documented that coyotes (*Canis latrans*) tolerated red foxes (*Vulpes vulpes*) in Yellowstone National Park during a high prey year, but not at other times. While cougars (*Puma concolor*) and bobcats (*Lynx rufus*) co- exist during summer, cougars killed bobcats when both species were forced to lower elevations in winter (Koehler and Hornocker, 1991). With smaller numbers of individuals left, an ecological specialist, EWs might thus be sensitive to competition from the AWs

1.4 The effect of competition on carnivores

The outcome of competition between carnivores may vary with factors such as potential of adaptation or specialization of competing species, body mass, patterns of group size and territorial ownership (Palomares and Caro 1999). Larger species usually dominate smaller size carnivores. For instance lions usually dominate the interaction with spotted hyaenas and wild dogs (Durant 2000). Similarly, group size is also

important factor influencing dominance between species. For instance, wild dogs manage to co-exist with spotted hyaenas due to their large group sizes that help them to adequately defend their kills (Darnell *et al.* 2014).

Competition may result in spatial or temporal avoidance, reductions in the density of the subordinate species, or even competitive exclusion from certain habitats or regions (Linnell and Strand 2000). For instance, wild dogs have been shown to avoid areas with high lion densities (Girman *et al.*, 1993; Creel and Creel 2002). Cheetahs (*Acinonyx jubatus*) in the Serengeti Park avoid habitat with the highest density of its main prey, Thomson's gazelle (*Gazella thomsoni*) because of the high density of lions or spotted hyaenas (Durant 1998; Creel 2001). Similarly, Arctic foxes (*Vulpes lagopus*) rarely use the area near to red fox (Rodnikova *et al.* 2011). Cheetahs density decline because of predation and competition with spotted hyenas and lions (Durant 2000). In Nepal, leopards (*Panthera pardus*) avoided habitats where tiger (*P. tigris*) densities were high (McDougal, 1988), while another study found a significant pattern of avoidance of spotted hyaenas by the smaller brown hyaenas (*Hyaena brunnea*; Mills1992). Interference competition among wolves and coyotes can influence the abundance and distribution of coyotes (Peterson 1995; Berger and Gese 2007). Regarding density, coyote abundance is documented to be limited by competition with wolves (Berger and Gese 2007) which was further confirmed by the increase of coyote populations across North America following wolf extermination (Peterson 1995).

Reintroduction of wild dogs into Etosha National Park, Namibia, failed possibly because of lion predation (Scheepers and Venzke 1995). The larger body sized tigers reportedly displaced leopards from its historic range in India? (Harihar *et al.* 2011; Odden et al. 2010). Because of the high energetic costs of hunting, wild dogs are suggested to avoid high density areas of spotted hyaenas where the risk of kleptoparasitism is high (Girman *et al.* 1993; Van der Meer 2011).

Competition can also cause local extinction (Silvestro *et al.* 2015). For instance, local extinctions of wild dogs were caused by lions or hyaenas where competition was intense (Vucetich & Creel 1999). In Etosha National Park, 71% of the hayena mortality was due to lions (Trinkel an Kastberger 2005). Caro (1994) reported that, in Serengeti National Park, lions killed entire cheetah litters, contributing to a survival rate at age two months of 29%. Further, red foxes were eradicated by arctic foxes in North America (Bailey *et al.* 1993).

1.5 Resource use and coexistence of sympatric carnivores

Currently niche partitioning is a major topic of research in community ecology and conservation (Fedriani *et al.* 2000; Milleret *et al.* 2018). This is because, sympatric species can coexist in a stable environment through partitioning diet, habitat or activity time to reduce competition (Schoener 1983; Durant 1998; Linnel and Strand 2000; Creel 2001; Trinkel and Kastberger 2005; Darnell, *et al.* 2014). For instance, in areas where AWs are sympatric with black-backed jackals and side-striped jackals, AWs use dry open grassland (Kingdon 1977), black-backed jackals use open woodland (Fuller *et al.* 1989) side-striped jackals use densely vegetated habitats (Fuller et al. 1989; Kingdon 1977; Smith 2018). Similarly, when the three species are sympatric, the peak activity time for AWs is during the day and for striped jackals during the night, while black backed jackals are more active at dawn (Fuller *et al.* 1989). However, there is no information about the resource use of AWs at locations where they are sympatric with EWs.

1.6 Anthropogenic impacts on carnivores

Carnivore conservation is a global challenge in the face of increasing human populations and associated land-use and land-cover changes (Bekoff and Mech 1984; Massolo and Meriggi 1998; Cayuela 2004; Zalewski *et al.* 2004; Athreya *et al.* 2013; Gebresenbet et al. 2018). For instance, human-induced habitat loss and fragmentation are forcing carnivores to inhabit ever-smaller areas, increasing the frequency of antagonistic interactions and disrupting the coexistence of carnivore species (Sinclair and Dobson 2015). Likewise, Afroalpine habitats in Ethiopia are geographically fragmented and facing a rapid ecological change due to continuous pressure from human activities and climate change (Spehn and Korner 2002; Lemenih and Teketay 2005; Kidane *et al.* 2012; Tolessa *et al.* 2017). These anthropogenic impacts (Fig. 2), leading to environmental resource degradation (Tolessa *et al.* 2017), increase human-carnivore conflict around protected areas

(Eshete 2018; Gebresenbet *et al.* 2018; Smith *et al.* 2018), which is the major causes for carnivore persecution.



Figure 2 Livestock (sheep, horses, donkeys, and cattle) in matrix habitat at Guassa Community Conservation Area.

Persecution due to livestock predation has been the major reason for eradicating carnivores from most of their former range (Musiani *et al.* 2003: Ripple 2014). For instance, due to persecution, the golden jackal, which had been the indigenous and common predatory species of Hungary and Greece until the end of the 19thC, was extirpated by the beginning of the 20thC (Szabó *et al.* 2009). In addition, the extermination of the Mexican wolf (*Canis lupus baileyi*) from its entire natural range by the 1970s (Brown 2007) and extinction of the Falkland Island wolf (*Dusicyon australis*) in 1876 (Sillero-Zubiri 2004) as a result of livestock predation are some examples. Moreover, conservation efforts can turn out to be insufficient when the predator has a negative impact on the economy of local communities (Cayuela 2004).

The AW can potentially be threatened by habitat loss and human persecution as a result of livestock predation. A study in the Serengeti showed that during their breeding time, AWs feed on larger wild prey, carcasses and sheep (Temu *et al.* 2018). Similarly, a study in Waza National Park, Cameroon, revealed that AWs attack small domestic livestock camouflaged in the tall grass during the dry season (Bauer 1999). In Ethiopia, studies on human-wildlife conflict have been limited to several localities, and those species that are considered livestock depredators could vary from

locality to locality (Yirga and Bauer 2010; Gebresenbet *et al.* 2018). Thus, assessing the situation surrounding livestock depredation incidents, economic loss due to wildlife, community attitudes toward wildlife and evaluating techniques that are used by communities to protect livestock will enhance carnivore conservation (Wang and Macdonald 2006; Schuette *et al.* 2013).

2. Aim of the study

The aim of this thesis was to document the behavioral ecology of African wolves (AWs) and to investigate the extent of competition between AWs and Ethiopian wolves (EWs) in the Ethiopian highlands. This thesis is based on tracking of 14-collared individuals, prey trapping, and use of the scat analysis.

The specific objectives of this study were to:

- Evaluate the extent of competition between AWs and EWs, inferred from tracking collared AWs and carrying out scat analysis
- 2. Investigate the foraging behavior of AWs from direct observation of collared AWs and capture of small mammals that contribute to their diet
- 3. Determine the home range, activity pattern and habitat use of AWs from the GPS locations of collared individuals
- 4. Investigate the status of human-carnivore conflict from scat analysis, interviews, and tracking collared wolves.

3. Main Methods

3.1 Study area

We conducted this study in two Ethiopian Afroalpine ecosystems (Fig. 3), Guassa-Menz Community Conservation Area (GCCA; $10^{0}15'-10^{0}27$ 'N; $39^{0}45'-39^{\circ}49$ 'E) and Borena Saynt Worehimenu National Park (BSNP; $10^{0}50'-10^{0}53'$ N; $38^{0}40'-38^{0}54'$ E), both in northern central Ethiopia. Afroalpine ecosystems in Ethiopia are home to a variety of plant (Nemomissa, 1998) and animal species (Estes 1991; Yalden and Largen 1992 ; Kingdon *et al.* 2013). The Ethiopian highlands are key center of biodiversity and endemism, in which about 70% of Africa's Afroalpine habitat is found, which is split into two main parts by African Rift Valley, northwestern and southwestern.

GCCA is an area of 111km^2 with an elevation ranging from 3200-3600m, managed by the Menz community as a common property resource, and is used for controlled livestock grazing and for the collection of firewood and grass (Ashenafi *et al.* 2005). Rainfall at GCCA averages 1650 ± 243 mm per year, average monthly temperature is 11.0 ± 1.2 °C, and mean monthly low and high temperatures are 4.3 ± 0.5 °C and 17.8 ± 0.3 °C, respectively (Fashing *et al.* 2014). BSNP is a legally protected area of Ethiopia with an area of 153km^2 and an elevation ranging from 1900- 3700m. The average annual rainfall is 2,000mm and the annual temperature ranges between 7.5 and 11°C (Eshete *et al.* 2018).

Based on the levels of anthropogenic disturbance, we divided each study area into three zones. These are *core* (the section of the protected areas where all human and livestock activities are prohibited), *buffer* (the section of the protected areas where controlled livestock grazing is permitted and areas used only for grazing adjacent to the protected area that used), and *matrix* (human-dominated areas adjacent to the protected area which consist mainly of farmland and settlements. In most Ethiopian protected areas, livestock grazing is a common practice (Stephens *et al.* 2001; Abebe and Bekele 2018). In addition to AW, some large mammalian species in both GCCA and BSNP are: EWs, gelada *(Theropithecus gelada),* spotted hyaena, and Starck's hare (*Lepus starcki*) (Fashing *et al.* 2014; Eshete *et al.* 2015).



Figure 3. Study areas, Borena Saynt Worehimenu National Park and Guassa Community Conservation Area. Inserts indicate locaitons for African wolf (green) and Ethiopian wolf (red).

3.2 Material and methods

3.2.1 Capture and immobilization of African wolves

Tracking AW individuals is critical to most of the data used in this thesis including foraging ecology, home range, habitat use and AW-EW behavioral interaction. Hence, we captured AWs using #3 rubber-lined Soft-Catch foothold traps (Woodstream Corporation, Lititz, Pennsylvania, USA). During each trapping session, four to eight traps stations were set up with sheep meat as

bait (Rowe-Rowe and Green 1981). Once trapped, the wolves were covered by a blanket and manually restrained for administration of 0.025 mg/kg of dexmedeto-midine followed by 8 mg/kg of ketamine based on estimated body weights. Details of the immobilization technique are given in the Appendix (Guetema et al. 2018). The captured individuals were fitted with VHF collars (Fig. 4).



а

b

Figure 4. Immobilized and collared African wolves (a) Team tracking African wolves in Guassa Menz Community Conservation Area (b).

3.2.2 Competition between African and Ethiopian wolves

Paper I was planned to investigate the interference and exploitative competition between AWs and the endangered EWs. The study was carried out based on focal watches on seven AW collared individuals from four packs in the GCCA. We used a hand-held directional antenna to locate respective animals, and followed them and carried out focal observations. Locations of the focal wolves were recorded at 30 min intervals during the daytime for a total of 3,864 h. For any interaction observed between the two wolf species, we recorded the nature of the interaction as neutral (both species present ignored one another), aggression, and aggression with bite. If the interaction was agonistic, we also determined the winner (i.e., which species chased the other away). For this data analysis, we used binomial logistic regression to analyse the outcome of winning the agonistic interaction (response variable: which species won in relation to the two sites (categorical explanatory variable: buffer zone and core area)) using the glm function. Given the low population sizes of both EWs and AWs and the fact that both species exhibit territoriality, it

is virtually certain that repeated sampling of the same individuals occurred; however, we were unable to account for this in the present study.

To compare the habitat overlap with AWs, we recorded EWs sightings walking along four transects (spaced at 1km and totalling 9km) thrice monthly. To determine the diet overlap, we collected 175 scats of AWs during the wet season (June–November) of 2015 and 175 scats during the dry season (December–May) of 2015–2016. The scats were dried and broken into pieces, and prey remains were identified via comparison with reference samples (Sillero-Zubiri and Gottelli 1995). Data on EW diet, based on frequency of occurrence in faeces, were obtained from a previous 12-month study by Ashenafi *et al.* (2005) at Guassa.

Because rodents are the main dietary item of EWs (Sillero-Zubiri and Gottelli 1995; Ashenafi *et al.* 2005), we studied the rodent density using Sherman live traps in the buffer zone and core area with 834 traps and 1181 traps respectively. Mole rat abundances were also estimated using random plots (Ashenafi *et al.* 2005). We baited the traps with peanut butter mixed with roasted barley flour and replenished them each day. We compared the abundance of each of the rodent species in both habitats using the generalized linear model, a logit link and binomial distribution. We compared Shannon's diversity indices (*H*) of rodent and shrew species of the core area and buffer zone by fitting a generalized linear mixed-effects model using the linear function in the line4 package.

3.2.3 Foraging ecology of African wolves

We needed data on AW foraging ecology to investigate to what extent AWs depend on rodents (both live hunting and scavenging), to compare the extent of competition with EWs. This study aim to answer if the high proportion of rodents recorded in scat analysis (paper 1) were from scavenging (dead animals) or live hunting. During the tracking of the collared AWs, we recorded their activities, including successful and unsuccessful feeding attempts. A successful attempt was scored if the prey was killed and ingested. Accordingly, an unsuccessful attempt was scored when they failed to capture and kill the prey.

To determine the percentage of hunted live rodents and scavenged items, we classified the food items consumed by AWs as hunted prey, livestock carcasses (cattle, horses, sheep and goats), and rodent carcasses (taken from *difit* traps). To identify the frequent feeding sites of AWs, whenever we observed AWs feeding or attempting to capture prey, we recorded the appropriate habitat type, classified as bushland, open grassland and farmland.

To evaluate the percentage of scavenged (dead rodents eaten) in the diet of AWs in the study area, assessments of the rodents killed by farmers are needed. In the Ethiopian highlands, farmers use a traditional trapping method known as '*difit*' (Fig. 5) to protect their crops from rodents. Difit are made of a locally manufactured rope, a relatively heavy stone and some barley seeds as bait. We collected data on the use of difit in GCCA, where 25 barley farm sites adjacent to GCCA were investigated, recording the number of rodents trapped (per hectare per day) and the extent to which AWs exploited the traps by taking the dead rodents. Every morning, after the traps were set we checked them regularly at 2 h intervals. When we found rodents had been caught in the trap, we recorded their number (usually one per trap, but occasionally two) and the species to which they belonged. We then cleared and reset the traps. We predicted the proportion of the food items consumed by the AW in relation to seasons (dry vs. wet) and prey items (rodents, insects, live sheep, and carcasses) using logistic regression. We also compared effect of habitat types on the efficiency of AWs in capturing rodents using logistic regression



Figure 5. A *difit* and captured rodent amidst crops on a farm. The end of the rope is tied to the barely (stem with seed). As the rodent feeds on the barley seed, the rope eventually breaks and released rock kills the rodent. (A=Rope, B= Barely stem and seed, C= dead rodent).

3.2.4 Ranging, habitat, and activity patterns of African wolves

The third paper focused on studies of the resource use (space and activity time) of AWs and compared the results with previous studies of EWs. From the GPS locations recorded during the tracking of the collared AWs, home range size of AWs was estimated using minimum convex polygon (MCP) and fixed kernel density estimation (KDE) methods using R. Similarly, we recorded activities of the observed wolf as travelling, resting, hunting, feeding, and social interaction.

To determine activity peaks we lumped activities into two categories: inactive (resting) and active (all other behaviours). For this analysis, the 24-hour cycle was divided into four discrete periods, 04:01–10:00 h (dawn-morning), 10:01–16:00h (midday), 16:01–22:00h (dusk-evening)22:01– 04:00 h (mid night) (Leuchtenberger et al. 2018). Sightings of radio-tagged AWs accompanied by conspecifics were also recorded. We considered animals to be in a group when they were <50 m from each other. We compared home range sizes of the two sites using linear models for 50% and 95% KDE separately. Site was a fixed effect with two levels (i.e. BSNP and GCCA), considering each individual as the sampling unit. We compared habitat preferences using general linear model 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. We estimated percentage time spent per hour in relation to activity with two levels (active and resting) and time (i.e. 24-hours cycle) using GLM. R version 3.5.1 (R Core Team 2015) for all analysis.

3.2.5 African wolf predation on livestock and associated conflict

For paper IV, we collected data through a semi-structured questionnaire employing during face- to-face interviews. We conducted a questionnaire survey of 250 randomly selected households for the number of livestock predated by carnivores (EW, AW, spotted hyaena and serval *Leptailurus serval*). The attitude of the respondents towards AWs and EWs (positive, negative or neutral) was

also queried during the survey. Households were also asked how they attempted to reduce livestock predation (with options of guarding more attentively, moving their sheep grazing system away from the AW habitat, reduction in sheep number and attacking wolves to minimize their number). The livestock shelter used by the local community during the night was recorded, and the number of livestock in each of the 250 households was counted during the early morning before the livestock were let out.

We studied the diet of the AW from scat analysis. To avoid confusion with scats of other canids, we collected samples from den sites of the AW in areas where EW and domestic dogs were not observed during the study period. For this scat analysis, similar methods as in paper II were followed.

4. Results and discussion

4.1 Competition between African and Ethiopian wolves

Paper I findings revealed interference competition with AW was a previously underappreciated potential threat to EWs in fragmented northern Ethiopian highland habitats. Of the 82 observed interactions between AWs and EWs, most (93.9%, N=82) were agonistic. The species winning the interaction depended on the site (buffer zone and core area) and group size of AWs. In the buffer zone, AW dominated the interactions, while EW dominated in the core area, which demonstrated territorial defence. In addition, group size helped AWs win some contests, a common pattern in many other carnivores (Merkle *et al.* 2009). From scat analysis, our findings suggested that AW were opportunistic foragers, consuming a more diverse diet including rodents (47.5%;n=642), insects, (11.2%), and livestock carcasses (17.2%)) which differed from the rodent specialist EWs (Marino 2003; Sillero-Zubiri and Gottelli 1995; Ashenafi *et al* 2005).

In GCCA, AWs mainly used the buffer (82.4%, n-252) while EW used the core zone (98%, n=3052). The study also revealed that rodent abundances and species compositions did not differ significantly between the core area and the buffer zone. This indicated that the use of the buffer zone by EWs may be constrained by interspecific competition, and not by the absence of suitable habitat and thus prevent population growth.

4. 2 Foraging ecology of African wolves

Paper II revealed that a large proportion of the rodents whose remains have been found in the scats of AWs (paper I) were from dead animals. For instance, among the 491 rodents consumed by AWs, 28% were hunted and 72% were scavenged from traps (*difit*) while EWs depend on hunting live rodents (Sillero-Zubiri and Macdonald Gottelli, 1995). This indicated that exploitative food competition between the AWs and EWs is probably limited. AWs had success rates of 21.1% (n=648) and 8.7% (n=23) in capturing live small rodents and mole rats, respectively. Foraging

rates on live rodent prey were higher in the farmlands (36%) than in the other habitat types (<17%). This might be among the reasons why AWs prefer areas in proximity to human settlements. Moreover, our study suggests that increasing human population and habitat loss may offer AWs a competitive advantage over EWs.

On the other hand, the study highlighted the importance of AWs in rodent pest control and waste management through their removal of rodent and livestock carcasses near farms in the Ethiopian Highlands. From the study area, the farmers trapped rodents to protect their farms ($24,0\pm6,6$ pest rodents per ha per day) during peak barley production (July to November) using local traps (*difit*) where ~81% of these captured pest rodents carcasses were collected by AWs and only 1% by EWs.

4.3 Ranging, habitat, and activity patterns of African wolves

Paper III reveals the significant variation in AW home range sizes in different landscapes in the Ethiopian highlands. We recorded larger home range size in BSNP (4.5 ± 1.5) compared to GCCA (2.2 ± 0.7 , 95% KDE). Previous studies from Bale Mountains National Park recorded a home range of 8.2km² KDE 95% (Admasu *et al.* 2004). This finding suggests there is considerable plasticity in space use among AWs, which may enhance the ability of AWs to respond to human-induced landscape changes. These results support the feeding behavior of AWs as ecological generalists who will benefit at the expense of EWs if intact habitat is not protected.

Paper III also demonstrates that AWs prefered areas in proximity to human habitats, which might be explained by the lower rodent hunting efficiency of AWs in intact habitat) (paper II) and abundance of anthropogenic resources around human settlement. In addition, AWs were active in the hours around dawn and dusk at both sites, unlike the sympatric EW, which was active during the day (i.e., diurnal) in the Ethiopian Highlands due to the diurnal activity patterns of the rodents that dominate their diet (Sillero-Zubiri and Gottelli 1995; Ashenafi *et al.* 2005; Eshete *et al.* 2018). To avoid human persecution during the day, AWs used bushland while they used farmland and open grasslands during the night.

In general, the findings of this paper indicate that niche partitioning between the AWs and the EWs might be among the factors enabling the coexistence of the two species in the Ethiopian highlands. However, with current trends in human population growth in the Ethiopian highlands (Tolessa *et al.* 2017), anthropogenic impacts may tend to facilitate competition between AWs and EWs, particularly in the fragmented habitats where AWs use the intact (undisturbed Afroalpine) habitat for protection from human attacks. Hence, the results support the emerging picture of AWs as ecological generalists who will proliferate at the expense of EWs if intact Afroalpine habitat is not protected. We assessed habitat by recording the habitat type within a 20-100 m radius of each location as woodland, bushland, open grassland, or agriculture.

4.4 African wolf predation on livestock and ensuing conflict

Paper IV demonstrated that AWs were the most important livestock predator, accounting for 74.6% of all reported kills (n = 492) and 78.9% of the economic losses. Thus, the community had negative attitudes toward the AWs (80.8% versus 14 % toward EWs), of which sheep accounted for 90% of the reported livestock killed. Highest livestock predation occurred during the dry season (70%: January–April), which might be due to the availability of dead rodents captured by 'difit' (paper II), low abundance of rodents (Paper IV) and reproduction time.

Consequently, most of the respondents (44%) suggested eliminating the AW as a solution to livestock losses, while others suggested more attentive guarding (35.6%) and reducing the number of sheep (15.6%). Mazzoli and Dunstone (2002) reported that livestock predation by mammalian carnivores was the most important reason for the global decline of wild carnivores. This negative attitude of the community toward AWs, affects their coexistence and in consequence pushes AWs towards habitat favoured by EWs, which may intensify the interference competition.

4.5 Appendix: Capture and immobilization of African wolves

While it is preferable to minimize the need to handle wild animals to obtain information for their study, important spatial and interspecific interaction information can only be collected through capture and immobilization (Brivio *et al.* 2015). From our experience AWs can be easily and safely captured using rubber–padded leg-hold traps which are also used for EWs (Sillero-Zubiri 1996; Ashenafi *et al.* 2005).. A combination of dexmedetomidine and ketamine was effective for immobilization of AWs without side effects on immobilized animals. Our study also indicated that AWs can be captured excluding the sympatric EW with prior knowledge of habitat and activity times of both species, with the best capturing time between 17:00-20:00h, which was found to be in line with the highest capture rate at both localiti

5. Conclusions and future recommendations

The knowledge generated by this study improves our understanding of AW interactions with EWs in both interference and exploitative competition. Our study demonstrated that in the Ethiopian Highlands, AWs can coexist with EWs through resource partitioning with limited exploitative competition. However, with its tolerance of disturbed habitat, AWs can be a threat for ecological specialist EWs through interference competition, particularly with the current increases of anthropogenic impacts around protected area of Ethiopian highlands. The study also found that AWs are omnivorous and opportunistic foragers, and their diet varies according to season (Paper- II, IV). They prefer areas in proximity to human settlement because they benefit from scavenging on anthropogenic resources (paper-III). The home range of AWs ranges from 2-8km² KDE 95% in different landscapes which indicates AW's flexibility in home range size, demonstrating their ability to respond to habitat fragmentation. (Paper-II).

This is the first detailed study on the behavioural ecology of AWs. We presented findings on interspecific competition with EWs, foraging behavior, spatial ecology of AWs in relation to EWs, and AW-human interactions. Further work should include studies on spatial and temporal activities of both wolf species in sympatry, population status of AW, reproductive and den site selection of both species.

Moreover, for future conservation work we posit that:

- 1) Reducing human encroachment and habitat loss in that fragmented habitat may offer the generalist AWs a competitive advantage over endangered EWs (Paper I),
- 2) local education efforts to highlight the complex role AWs play in highland ecosystems to reduce their persecution (Paper II and IV), and
- 3) protection of intact habitats to preserve habitat preferred by EWs (paper I

6. Project in progress

6.1 Population status and reproduction ecology of African wolves

As continuation of Paper I and paper IV, study of AW density and reproduction ecology is ongoing. The group size of AWs is likely to be the major limiting factor in relation to competition with EWs (Paper I). On the other hand, with little education and low enforcement for the AW, its population size in the GCCA is likely to be controlled by the local community who eliminate pups whenever a den is located. Such lethal control has been widely reported as a response to depredation in a range of communities leading to severe population declines in many large carnivore species. To estimate the density of AWs, we are using call-up methods in four Ethiopian Highlands (Bale Mountains, Arsi Mountains, GCCA and BSNP).

Regarding reproduction ecology, we are recoding any active den sites found (Person and Russell 2009), number of pups observed and activities of parents with pups. To evaluate den site selection, we are characterizing den site, threats, species of plants around the den, distance from fresh water, distance to road, distance to nearest human disturbance, direction of the main hole, distance from village, canopy closure of each den site and status of human disturbance (Theuerkauf *et al.* 2003). Better understanding the population status of AWs and their reproduction ecology will have important connotaitons for the conservation of the Endangered EWs and human-carnivore conflict mitigation in the Ethiopian Highlands.

6.2 Promoting the Co-Existence Approaches to Carnivore Conservation

In order to reduce human-carnivore conflict and promote co-existence with AWs and EWs, our experience points to a prioritization of local education efforts. AWs cause economic damage to local farmers through livestock predation (paper-IV), they also appear to play an important role in scavenging pest rodents among farmlands (Paper-II). Thus, we have initiated the project to increase the community awareness toward the value of AWs and other carnivore species. (https://www.rufford.org/projects/tariku_mekonnen_gutema

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Author for correspondence:

Nils C. Stenseth e-mail: n.c.stenseth@ibv.uio.no

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Competition between sympatric wolf taxa: an example involving African and Ethiopian wolves

Tariku Mekonnen Gutema^{1,2}, Anagaw Atickem³, Afework Bekele⁴, Claudio Sillero-Zubiri^{5,6}, Mohammed Kasso⁴, Diress Tsegaye⁷, Vivek V. Venkataraman⁸, Peter J. Fashing⁹, Dietmar Zinner³ and Nils C. Stenseth^{1,4}

¹Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, PO Box 1066, Blindern, 0316 Oslo, Norway ²Department of Natural Resources Management, Jimma University, PO Box 307, Jimma, Ethiopia ³Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany ⁴Department of Zoological Sciences, Addis Ababa University, PO Box 1176, Addis Ababa, Ethiopia ⁵Wildlife Conservation Research Unit, Zoology Department, University of Oxford, Tubney House, Tubney, UK ⁶ IUCN SSC Canid Specialist Group, Oxford, UK ⁷Department of Biosciences, University of Oslo, PO Box 1066, Blindern, 0316 Oslo, Norway ⁸Department of Human Evolutionary Biology, Harvard University, 11 Divinity Avenue, Cambridge, MA 02138, USA ⁹Department of Anthropology and Environmental Studies Program, California State University Fullerton, 800 North State College Boulevard, Fullerton, CA 92834, USA

DZ, 0000-0003-3967-8014; NCS, 0000-0002-1591-5399

Carnivore populations are declining globally due to range contraction, persecution and prey depletion. One consequence of these patterns is increased range and niche overlap with other carnivores, and thus an elevated potential for competitive exclusion. Here, we document competition between an endangered canid, the Ethiopian wolf (EW), and the newly discovered African wolf (AW) in central Ethiopia. The diet of the ecological specialist EW was dominated by rodents, whereas the AW consumed a more diverse diet also including insects and non-rodent mammals. EWs used predominantly intact habitat, whereas AWs used mostly areas disturbed

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by humans and their livestock. We observed 82 encounters between the two species, of which 94% were agonistic. The outcomes of agonistic encounters followed a territory-specific dominance pattern, with EWs dominating in intact habitat and AWs in human-disturbed areas. For AWs, the likelihood of winning encounters also increased with group size. Rodent species consumed by EWs were also available in the human-disturbed areas, suggesting that these areas could be suitable habitat for EWs if AWs were not present. Increasing human encroachment not only affects the prey base of EWs, but also may impact their survival by intensifying competition with sympatric AWs.

1. Introduction

Carnivore species have coexisted for millennia in many of Earth's ecosystems through temporal, spatial or dietary niche partitioning [1,2]. Over the past several decades, however, herbivore prey depletion resulting from hunting by humans and habitat destruction disrupted their adaptations for coexistence [3]. As a result, many carnivore species face extinction risk because of elevated interspecific competition in shrinking and degraded habitats [4,5]. This competition can take the form of direct lethal encounters, interference competition at kills, exploitative competition over diminished prey populations, exclusion of one species by another from areas of high prey density and fear-mediated shifts to less optimal habitats [2,5].

Two Canidae species, African wolves (*Canis lupaster*) and endangered Ethiopian wolves (*Canis simensis*), coexist in parts of the Ethiopian Highlands [6]. With fewer than 500 adult individuals left in the wild, the Ethiopian wolf (EW) is the world's rarest canid [7]. The African wolf (AW), which was until recently incorrectly regarded as a golden jackal (*C. aureus*) [8], is distributed in northern and eastern Africa [9]. As an ecological specialist and solitary forager with a small population size [6], the EW may be particularly sensitive to the impacts of interference competition from the AW, especially in light of recent preliminary evidence of partial dietary overlap between the two species [10]. Here, we aim to assess dietary overlap, habitat quality and whether interference competition occurs between EWs and AWs in north central Ethiopia.

Relative body mass, group size and territorial ownership are typically the most important factors in determining the outcome of agonistic encounters between carnivores [4,5]. Based on these considerations, EWs (males: 14.2–19.3 kg, females: 11.2–14.2 kg; [11]) should dominate the smaller AWs (males: 9.0 kg, females: 8.1 kg; [12]) in one-on-one agonistic encounters. By recording behavioural interactions in two ecologically distinct zones (buffer zone and core area), we were able to assess the relative importance of these factors in determining the outcome of interactions. This has crucial consequences for understanding potential conservation threats posed to the endangered EW by the AW if both species are forced to share more of their shrinking and degraded habitats across the Ethiopian Highlands.

2. Material and methods

2.1. Study site

The study was carried out within the Guassa Community Conservation Area (GCCA; figure 1). GCCA contains an unusually intact Afroalpine grassland ecosystem with an estimated 21 EW individuals [13,14]. We delineated the study area into three zones: core area (section of GCCA where all human and livestock activities are prohibited), buffer zone (section of GCCA where controlled livestock grazing is permitted) and *matrix* (human-dominated areas adjacent to GCCA consisting mostly of farmland and settlements) (figure 2). We focused our study on the 30 km² southern portion of the GCCA, within which we regularly spotted eight EWs and 21 AWs.

2.2. Observational data collection

Seven AWs from four packs were captured using rubber-padded leg-hold traps and fitted with very high frequency collars (for detailed procedures, see Gutema *et al.* [12]). We used a hand-held directional antenna to locate respective animals, followed them and did focal observations. Locations of the focal



Figure 1. (*a*) Distribution of the seven remaining populations of Ethiopian wolves in the Ethiopian highlands and their respective population sizes (6 = current study area). (*b*) Map of Guassa within the Menz Highlands, north central Ethiopia. The population estimates here are from Marino & Sillero-Zubiri [7].

wolves were recorded at 30 min intervals during the day time for a total of 3864h (772.8 ± 323 h) [13]. Data from two collared individuals were excluded from the analysis. One of these individuals was found dead, possibly killed by humans. The other individual was lost during the third month of study when its signal disappeared.

Whenever the two wolf species were observed within approximately 120 m of one another, we recorded the nature of the interaction (neutral, aggression and aggression with bite), the number of individuals of each species present, and the duration and location of the interaction (core area or buffer zone) (cf. [15]). If the interaction was agonistic, we also determined the winner (i.e. which species chased the other away). A *neutral* interaction was recorded if all individuals of both species present ignored one another, an *aggression* was recorded if at least one individual of one species ran towards a member of the other species in an aggressive manner, and an *aggression with bite* was recorded if one or more individuals of one species bit a member of the other species. We used binomial logistic regression to analyse the outcome of winning the agonistic interaction (response variable: which species won in relation to the two sites (categorical explanatory variable: buffer zone and core area)) using the glm function. Given the low population sizes of both EWs and AWs and the fact that both species exhibit territoriality, it is virtually certain that repeated sampling of the same individuals occurred; however, we were unable to account for this in the present study.

2.3. Wolf diet

From June to November 2015 and December 2015 to May 2016, EW sightings were recorded while systematically walking four transects (totalling 9 km) thrice monthly. Transects were spaced at intervals of 1 km (figure 2). Since a previous study on the AW diet at Guassa was only based on a three-month study of scats (n = 101; [10]), we collected 175 scats during the wet season (June–November) of 2015 and 175 scats during the dry season (December–May) of 2015–2016. The scats were dried and broken into pieces, and prey remains were identified via comparison with reference samples [6]. Data on EW diet, based on frequency of occurrence in faeces, were obtained from a previous 12-month study by Ashenafi *et al.* [13] at Guassa.



Figure 2. The study area in the southern section of the Guassa Community Conservation Area, including transects (vertical lines) and sighting locations of AWs and EWs. The locations and outcomes of AW–EW encounters are also depicted. The dark grey area indicates the core area, the light grey area indicates the buffer zone and the white area indicates the matrix.

2.4. Habitat quality estimate

As a proxy for habitat quality, we used rodent density because rodents constitute a major part of the wolves' diet. Rodents were captured from both the buffer zone and the core area using Sherman live traps [16,17] to determine the habitat quality for the EW. Six and eight square grids of 5625 m^2 ($75 \text{ m} \times 75 \text{ m}$)



Figure 3. Fraction of agonistic encounters won by AWs and EWs in relation to encounter locations (buffer zone versus core area).

were established in the buffer zone and core area, respectively. A total of 2015 traps were set (834 traps in the buffer zone: 534 during the dry season and 300 during the wet season; 1181 traps in the core area: 431 during the dry season and 750 during the wet season). Trap stations were marked by coloured plastic tags on nearby vegetation to easily locate the traps during checking and collection. The traps were baited with peanut butter mixed with roasted barley flour and replenished each day. The traps were checked twice a day: during the early morning (6.30 to 8.30) and the late afternoon (16.30 to 18.30). They were set for a total of 75 h in each grid during both seasons. The abundance of each of the rodent species in both habitats were compared using the generalized linear model, a logit link and binomial distribution. We compared Shannon's diversity indices (H) of rodent and shrew species of the core area and buffer zone by fitting a generalized linear mixed-effects model using the lmer function in the lme4 package. Average Shannon's diversity for each one of the grids in 2015 trap sampling sessions from the two sites was used as the response variable, trapping locations as the random effect and habitat (buffer zone or core area) as the fixed effect. We estimated the abundance of the common mole rat, Tachyoryctes splendens, by counting active burrows in the buffer zone and the core area [13]. A total of 51 and 39 plots $(20 \text{ m} \times 20 \text{ m})$ in the buffer zone and the core area, respectively, on the transects established for sighting AWs were randomly selected to be checked for active burrows. The mole rat abundances in the two study zones were compared using generalized linear mixed models with mole rat presence/abundance as response variables, plots as the random effect and habitat (buffer zone or core area) as the fixed effect.

3. Results

3.1. Wolf interactions

AWs intensively used the buffer zone (57.2%) and matrix (40.8%), but only rarely (2.0%) entered the core area (total sightings: n = 3052; electronic supplementary material, table S1). By contrast, EWs were observed mostly in the core area (82.4%), though occasionally in the buffer zone (18.6%) as well (total sightings: n = 252).

Within 12 months, we observed 82 interactions between AWs and EWs, of which 58 (70.7%) occurred in the buffer zone while 24 (29.3%) took place in the core area. With the exception of five neutral interactions (6.1%), all others were agonistic (93.9%). Of the 55 agonistic interactions in the buffer zone, 52 (94.5%) were won by AWs and only 3 (5.5%) by EWs (Z = -3.11, p = 0.002; figure 3). Conversely, of the 25 agonistic interactions in the core area, EWs won 23 (92.0%), whereas AWs won only 2 (8.0%) (Z = 5.42, p = 0.001). On three occasions (in the buffer zone), an AW not only chased but also bit an EW. The likelihood of AWs winning agonistic interactions increased with group size (Z = 2.45, p = 0.01), while group size had no effect on whether EWs won interactions (Z = 0.45, p = 0.12; table 1).

The average duration per interaction was 3.1 ± 2.8 min (range 0.5–20 min; n = 82). The mean number of AWs involved per interaction was 1.9 ± 0.8 (range: 1–5), while EWs were more often solitary (mean 1.3 ± 0.4 ; range: 1–3).

Table 1. Estimates of probability of the AW versus EW winning encounters in core area versus buffer zone. 'Buffer zone' was used as a reference level in the analysis.

effects	estimate	s.e.	Ζ	p
intercept	1.150	1.808	0.636	0.250
site (core versus buffer)	—8.971	3.043	-2.948	0.003
AW group size	3.171	1.295	2.449	0.014
EW group size	2.001	1.300	—1.590	0.124

Table 2. Seasonal differences in the frequency of occurrence (FO) of food items in the diet of African wolves at Guassa as determined by scat analysis.

	dry (<i>n</i>	dry (<i>n</i> = 175)		wet ($n = 175$)		combined	
food items	n	% F0	n	% F0	n	% F0	
rodents	164	53.2	137	42.0	301	47.2	
Ethiopian hares (<i>Lepus fagani</i>)	5	1.6	9	2.8	14	2.2	
livestock (hunted or scavenged)	24	7.8	85	26.1	109	17.2	
duikers	0	0.0	3	0.9	3	0.5	
wild birds	7	2.3	5	1.5	12	1.9	
domestic chickens	0	0.0	7	2.1	7	1.1	
unidentified bones	31	10.1	25	7.7	56	8.9	
insects (mostly grasshoppers)	46	14.9	25	7.7	71	11.2	
graminoids	14	4.5	3	0.9	17	2.7	
potatoes	6	1.9	2	0.6	8	1.2	
soil	11	3.5	25	7.7	36	5.7	
total	308	100	326	100	634	100	

3.2. Diet

Based on faecal analyses, rodents (47.5%; n = 642) were the top prey items of AWs, followed by livestock (cattle and sheep) remains obtained via predation or scavenging (17.2%), and by insects (11.2%), usually grasshoppers (table 2). Rodents occurred in 93.0% of EW scat samples [13], which is significantly higher than the proportion of rodents (47.2%) in AW scat samples (t = 4.939, p < 0.001).

3.3. Prey density

From trapping, we obtained 522 small mammals, including nine rodent and two shrew species (table 3). There were no significant differences in species abundance of small mammals except two species, *Lophuromys brevicaudus* and *Stenocephalemys albocaudata*, which have higher abundance in the core area (table 4). No significant difference in species diversity was found between the buffer zone and core areas (electronic supplementary material, table S2). The abundance of active burrows of mole rats, a primary prey item of EWs, did not vary significantly between the core area (mean = 0.57, s.d. = 0.50, n = 51) and the buffer zone (mean = 0.44, s.d. = 0.50, n = 39; Z = -1.24, p = 0.21; electronic supplementary material, table S3).

4. Discussion

Disease, including rabies and canine distemper virus, is the most immediate threat to the survival of EWs in Bale Mountains National Park, which contains the largest and most extensively studied population [18]. Our study at Guassa reveals interspecific competition as another potential threat to EWs.

Table 3. Relative frequency (%) of rodent and shrew species trapped in the buffer zone and the core area during dry and wet seasons. Buffer zone: 834 traps, 534 dry season and 300 wet season; core area: 1181 traps: 431 dry season and 750 wet season.

	buffer zone		core area		
species	dry	wet	dry	wet	
Lophuromys brevicaudus	3.56	9.33	12.06	20.80	
Stenocephalemys griseicauda	5.81	0.00	0.00	2.13	
Stenocephalemys albipes	4.87	0.00	0.00	0.00	
Stenocephalemys albocaudata	0.00	7.33	3.25	7.73	
Mastomys natalensis	2.43	0.00	0.00	0.00	
Otomys typus	0.19	3.00	0.93	0.93	
Lophuromys flavopunctatus	1.12	2.00	0.00	2.53	
Dendromus lovati	0.00	0.00	0.23	0.00	
Arvicanthis abyssinicus	0.37	0.00	0.00	0.00	
Crocidura baileyi	0.00	0.00	0.23	2.40	
Crocidura macmillani	0.37	0.00	0.23	1.33	

Table 4. Rodent species abundance compared between the buffer zone and the core area (rodent species presence/absence as a response variable, habitat (buffer zone and core area) as fixed effect and traps as random variables). 'Core area' was used as a reference level in the analysis.

species		estimate	s.e.	Ζ	p
Lophuromys brevicaudus	intercept	—3.0699	0.1681	—18.257	$<\!\!2 imes 10^{-16}$
	core area	1.7036	0.183	9.307	<0.001
Stenocephalemys griseicauda	intercept	—4.2268	0.2908	—14.54	$<\!\!2 imes 10^{-16}$
	core area	0.393	0.3541	1.11	0.267
Stenocephalemys albipes	intercept	—3.6562	0.221	—16.543	$<\!\!2 imes 10^{-16}$
	core area	—0.3554	0.312	—1.139	0.255
Stenocephalemys albocaudata	intercept	—4.2268	0.2908	—14.536	$<\!\!2 imes 10^{-16}$
	core area	1.4923	0.3152	4.735	<0.001
Mastomys natalensis	intercept	—4.7719	0.3796	—12.572	$<\!\!2 imes 10^{-16}$
	core area	-0.3504	0.5364	-0.653	0.514
Otomys typus	intercept	—4.9273	0.4097	—12.027	$<\!\!2 imes 10^{-16}$
	core area	0.2604	0.5095	0.511	0.609
Lophuromys flavopunctatus	intercept	-4.9273	0.4097	—12.027	$<\!\!2 imes 10^{-16}$
	core area	0.8659	0.4677	1.852	0.0641
Crocidura macmillani	intercept	—6.725	1.001	—6.721	$1.80 imes 10^{-11}$
	core area	1.448	1.081	1.339	0.18

AWs inhabit the buffer zone and surrounding human-dominated landscape at Guassa, while EWs predominantly inhabit the core area of the protected area. AWs dominated interactions in the buffer zone, whereas EWs dominated in the core area, indicating that both species defended their territories. The outcome of interactions was affected by territorial dominance and numerical superiority which played a more important role than body size differences. Group size advantage in interspecific competition is common in carnivores [19–21]. Although no intraguild predation or prolonged physical fighting was observed, the three occasions of brief physical contact we observed involved biting, revealing the potential for interspecific disease transmission. Close spatial proximity also increases the likelihood of hybridization [22,23].

The EW is a rodent specialist which mainly foraged in the core area, while the AW is an opportunistic forager that regularly consumes livestock, and is thus relatively tolerant of habitat alteration by humans. Nevertheless, although AWs sometimes preyed on livestock and fed on insects and other non-rodent foods, rodents were still the top food item of AWs. This finding suggests the possibility of exploitative competition between AWs and EWs. Rodent abundances and species compositions did not differ significantly between the core area and the buffer zone, suggesting that, in the absence of AWs, EWs could also exploit the buffer zone habitat, which could facilitate an increase in EW population size. This result implies that the use of degraded habitats by EWs may be constrained by interspecific competition, and not merely by the absence of suitable habitat, and thus prevent EWs from range expansion and population growth.

5. Conclusion

AWs predominantly inhabit the buffer zone, a human-dominated landscape, while EWs mostly use the more intact core area at Guassa. The diets of EWs and AWs overlap, but AWs exhibit much wider dietary breadth. Patterns of interspecific interaction imply that each species engages in territorial defence against the other. Our study calls attention to the behavioural mechanisms that underlie competition between EWs and AWs, suggesting that increasing human encroachment and habitat loss may offer AWs a competitive advantage over EWs. EW conservation efforts would thus benefit from concurrent monitoring of AW populations where the two taxa co-occur.

Ethics. Ethiopian Wildlife Conservation Authority (EWCA) guidelines have been followed.

Data accessibility. Data available at the Dryad Digital Repository: (http://dx.doi.org/10.5061/dryad.vj2nn) [24].

Authors' contributions. T.M.G., A.A. and N.C.S. conceived the study. T.M.G. carried out the fieldwork. All authors contributed to data analyses, interpretation of results and writing the manuscript.

Competing interests. We declare we have no competing interests.

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Author for correspondence:

Nils C. Stenseth e-mail: n.c.stenseth@ibv.uio.no

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Foraging ecology of African wolves (*Canis lupaster*) and its implications for the conservation of Ethiopian wolves (*Canis simensis*)

Tariku Mekonnen Gutema^{1,3}, Anagaw Atickem^{4,5}, Diress Tsegaye², Afework Bekele⁵, Claudio Sillero-Zubiri^{6,7}, Jorgelina Marino^{6,7}, Mohammed Kasso⁵, Vivek V. Venkataraman⁸, Peter J. Fashing^{1,9} and Nils C. Stenseth^{1,5}

¹Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, and ²Department of Biosciences, University of Oslo, PO Box 1066, Blindern, 0316 Oslo, Norway

³Department of Natural Resources Management, Jimma University, PO Box 307, Ethiopia ⁴Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany

⁵Department of Zoological Sciences, Addis Ababa University, PO Box 1176, Addis Ababa, Ethiopia

⁶Wildlife Conservation Research Unit, Zoology Department, University of Oxford, Tubney House, Tubney OX13 5QL, UK

⁷IUCN SSC Canid Specialist Group, Oxford, UK

⁸Institute for Advanced Study in Toulouse, Toulouse 31000, France

⁹Department of Anthropology and Environmental Studies Program,

California State University Fullerton, 800 North State College Boulevard, Fullerton, CA 92834, USA

IVV, 0000-0001-5016-4423; NCS, 0000-0002-1591-5399

African wolves (AWs) are sympatric with endangered Ethiopian wolves (EWs) in parts of their range. Scat analyses have suggested a dietary overlap between AWs and EWs, raising the potential for exploitative competition, and a possible conservation threat to EWs. However, in contrast to that of the well-studied EW, the foraging ecology of AWs remains poorly characterized. Accordingly, we studied the foraging ecology of radio-collared AWs (n = 11 individuals) at two localities with varying levels of anthropogenic disturbance in the Ethiopian Highlands, the Guassa-Menz Community Conservation Area (GMCCA) and Borena-Saynt

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National Park (BSNP), accumulating 845 h of focal observation across 2952 feeding events. We also monitored rodent abundance and rodent trapping activity by local farmers who experience conflict with AWs. The AW diet consisted largely of rodents (22.0%), insects (24.8%), and goats and sheep (24.3%). Of the total rodents captured by farmers using local traps during peak barley production (July to November) in GMCCA, averaging 24.7 ± 8.5 rodents/hectare/day, 81% (N = 3009) were scavenged by AWs. Further, of all the rodents consumed by AWs, most (74%) were carcasses. These results reveal complex interactions between AWs and local farmers, and highlight the scavenging niche occupied by AWs in anthropogenically altered landscapes in contrast to the active hunting exhibited by EWs in more intact habitats. While AWs cause economic damage to local farmers through livestock predation, they appear to play an important role in scavenging pest rodents among farmlands, a pattern of behaviour which likely mitigates direct and indirect competition with EWs. We suggest two routes to promote the coexistence of AWs and EWs in the Ethiopian highlands: local education efforts highlighting the complex role AWs play in highland ecosystems to reduce their persecution, and enforced protection of intact habitats to preserve habitat preferred by EWs.

1. Introduction

The midsize canids in northern Africa considered to be golden jackals (*Canis aureus*) were recently reclassified as African wolves (AWs), *Canis lupaster*, due to their close phylogenetic relationship to the grey wolf (*C. lupus*) [1,2]. AWs are found throughout the Ethiopian Highlands, often in sympatry with endangered Ethiopian wolves (EWs), *Canis simensis* [3,4], Africa's most threatened carnivore. At fewer than 500 individuals, the EW is the rarest canid in the world [5]. Restricted to several enclaves of Afro-alpine habitats, small EW populations are highly vulnerable to extinction, particularly because of habitat loss as well as rabies and canine distemper virus outbreaks stemming from interactions with local domestic animals [6,7].

Recent scat analyses revealed that the diet of AWs consists largely of rodents (48–57%) and varies by season [8,9]. Given that EWs depend on abundant rodent populations for their survival and reproduction [10–12], potential niche overlap and competition between these two species might have negative effects on EW populations. Based on intensive study at multiple sites, EWs are known to be active rodent hunters and only rarely kill livestock or scavenge [10,11]. However, because our knowledge of the diet of AWs in the Ethiopian Highlands is based primarily on scat analyses [8,9], we do not know the proportion of rodents acquired through hunting versus scavenging rodents killed by local farmers using traditional practices. To better understand the nature and extent of potential competition between EWs and AWs, it is necessary to learn more about the AW's diet. If AWs primarily scavenge rodents, direct exploitative competition between these species may be relatively minor. On the other hand, if AWs primarily engage in the active hunting of rodents, particularly where the two species overlap, the potential for competition may be significant. Recent work has indicated that sympatric AWs and EWs do actively defend their territories from each other via agonistic interactions [8].

A better characterization of AW foraging ecology will also permit inferences about the nature of human-wildlife conflict in the Ethiopian Highlands. AWs are presently considered one of the main livestock predators in the Ethiopian Highlands and are heavily persecuted [9]. However, they may also provide an ecological benefit to farmers if they feed upon pests such as rodents and insects, which cause significant damage to crops in small-holder farms in Ethiopia [13–16].

Accordingly, our goal is to evaluate the foraging ecology of AWs in greater detail than before and to assess the potential effects their dietary choices may have on EWs via competition for resources. We intensively studied the foraging ecology of the AW in the Ethiopian Highlands via direct observations of 11 radio-collared individuals at two sites, and compared our results with those from published studies of the diet and foraging behaviour of EWs. Specifically, we estimated (1) the proportion of rodents in the diet of the AW that derived from scavenging versus predation, (2) the extent to which AWs foraged in farmland versus intact habitat and (3) rodent abundance and level of trapping activity by local farmers who experience conflict with AWs due to sheep predation.



Figure 1. Study localities, (1) Borena-Saynt National Park (BSNP) and (2) Guassa-Menz Community Conservation Area (GMCCA).

2. Methods

2.1. Study area

Our study was carried out in Guassa-Menz Community Conservation Area (GMCCA; $10^{\circ}15'-10^{\circ}27'$ N to $39^{\circ}45'-39^{\circ}49'$ E) and Borena-Saynt National Park (BSNP; $10^{\circ}50'-10^{\circ}53'$ N to $38^{\circ}40'-38^{\circ}54'$ E; figure 1), areas of Afro-alpine habitat located in the north-central highlands of Ethiopia. GMCCA spans 111 km² with an elevational range of 3200-3600 m [17], while BSNP covers an area of 153 km² with an elevational range of 1900-3700 m [18,19]. Both sites are also home to several mammal species endemic to the Ethiopian Highlands, including EWs, gelada monkeys (*Theropithecus gelada*) and Starck's hare (*Lepus starcki*) [11,18]. The Ethiopian wolf populations are estimated at approximately 21 individuals in GMCCA [11] and approximately 16 individuals in BSNP [5]. The local people in both areas are mostly agro-pastoralists who grow barley between June and November and keep a variety of livestock (mostly sheep but also goats, cattle and horses) [8,18]. The two study areas are 150 km apart, but their climates are broadly similar, with a wet season extending from June to November and a dry season from December to May [8,11,19]. Detailed climatic data are available only for GMCCA where rainfall averages 1650 ± 243 mm per year, average monthly temperature is $11.0 \pm 1.2^{\circ}$ C, and mean monthly low and high temperatures are $4.3 \pm 0.5^{\circ}$ C and $17.8 \pm 0.3^{\circ}$ C, respectively (n = 6 years) [17].

Livestock grazing is a common practice in most Ethiopian protected areas [20,21]. Based on the levels of anthropogenic disturbance, we divided each study area into three zones: *core* (the section of the protected areas where all human and livestock activities are prohibited), *buffer* (the section of the protected areas where controlled livestock grazing is permitted), and *matrix* (human-dominated areas adjacent to the protected area which consist mainly of farmland and settlements [8]). In GMCCA, EWs largely occupy the core while AWs mostly use the buffer zone [8].

2.2. Foraging behaviour

We captured 11 AWs using rubber-lined Soft Catch foothold traps (Woodstream Corporation, Lititz, Pennsylvania, USA) sizes 1.5 and 3 (for method details see [19]) and fitted them with VHF radio collars; two males and three females in GMCCA and three males and three females in BSNP (for more details see [19]). In the wet and dry seasons of 2016 and 2017, we followed collared individuals for 3–4 days per month during both day and night. Focal observations were carried out with

binoculars from distances of 50–150 m after locating the focal individuals using a hand-held directional antenna. We recorded their activity, including successful and unsuccessful feeding attempts. A successful attempt was scored if the prey was killed and ingested. Accordingly, an unsuccessful attempt was scored when they failed to capture and kill the prey [22]. Scavenging was defined as feeding on a dead animal, typically taking dead rodents from traps set by farmers (*difit*, see below) ([10,11]; electronic supplementary material, table S1). We classified the food items consumed by AWs as hunted prey (including common molerats *Tachyoryctes splendens*, smaller rodents, and shrews), livestock carcasses (cattle, horses, sheep and goats), rodent carcasses (taken from *difit* traps) and arthropods (mainly grasshoppers, but also spiders and beetles). Whenever we observed AWs feeding or attempting to capture prey, we recorded the appropriate habitat type, classified as bushland (greater than 50% shrubs, predominantly *Helichrysum* and *Erica* spp.), grassland (greater than 50% open land; including rocky grassland, open grazing land dominated by *Festuca* spp.) or farmland (barley and other crops).

2.3. Traditional traps 'difit' as a source of rodents for AWs

In both GMCCA and BSNP, farmers use a traditional trapping method known as *difit* to protect their crops from rodents [9]. However, for this specific objective, we collected data only from GMCCA. *Difit* are made of a locally manufactured rope, a relatively heavy stone and some barley seeds as bait (electronic supplementary material, figure S1). We collected data on the use of *difit* in GMCCA, where 25 barley farm sites adjacent to GMCCA were investigated, recording the number of rodents trapped (per hectare per day) and the extent to which AWs exploited the traps by taking the dead rodents. Farmers usually set up their traps in the morning (07.00–9.00 h), visiting them at 1–4 h intervals and resetting them if a capture had taken place. Trapping concluded in the evening (17.00–18.00 h). Every morning, after the traps were set we checked them regularly at 2 h intervals. When we found rodents had been caught in the trap, we recorded their number (usually one per trap, but occasionally two) and the species to which they belonged. We then cleared and reset the traps.

2.4. Data analysis

We compared the proportions of food items consumed by the AWs in the GMCCA and BSNP by a mixed effect model using food items as response variable, localities as fixed effects and individual collared animals as random effects.

We estimated successful hunting by AWs on two food classes (rodents and sheep) in relation to seasons, using logistic regression by fitting a general linear model. The response variable was binomial (1/0), indicating successful or unsuccessful hunting attempts, respectively. The fixed effects were diet (at two levels: rodents and sheep) and season (at two levels: dry and wet). We combined the data collected from GMCCA and BSNP (proportion of food items consumed) after verifying no significant differences for the two sites using one-way ANOVA followed by Tukeys's HSD post hoc test.

We also compared the effect of habitat types (i.e. fixed effect factor at three levels: bushland, farmland and grassland) on the success probability (attempt to feed and outcome) of AWs capturing rodents (i.e. binomial response variable: 1/0 where 1 is successful) using logistic regression.

All analyses were done in R v. 3.3.1 (R Core Team 2016).

3. Results

3.1. Foraging ecology observations

We observed radio-tracked AWs for 845 h across 16 months during 2016 and 2017 (392 h in GMCCA and 453 h in BSNP) resulting in a total of 2952 records of food items. Our focal observations revealed that the proportion of food items consumed by AWs in both study areas did not differ (electronic supplementary material, table S3). We found that AWs consumed primarily rodents during the wet season, and ate a more diverse diet, including more insects, livestock carcasses and sheep, during the dry season (figure 2 and table 1). Indeed, dietary composition differed significantly between the wet and dry seasons: rodents (z = 94.6, d.f. = 1, p < 0.001), sheep (z = 22.4, d.f. = 1, p < 0.001) and insects (z = 38.6, d.f. = 1, p < 0.001). The probability of AWs successfully hunting rodents (successful events as a



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Figure 2. Probability of African wolves feeding on different diets in the dry and wet seasons.

Table 1. Composition of African wolf diet. Recorded as successful hunting attempts from focal animal observations of 11 individuals in GMCCA and BSNP.

		BSNP	BSNP			GMCCA			
food items	total n = 2952	dry n = 902	wet <i>n</i> = 753	total <i>n</i> = 1655	dry n = 450	wet <i>n</i> = 847	total <i>n</i> = 1297		
small rodents	22.76	16.30	31.08	23.02	11.56	28.22	22.44		
arthropods	19.00	26.72	17.00	22.30	18.44	12.87	14.80		
livestock	18.56	20.51	14.48	17.76	29.78	14.17	19.58		
caracasses									
unidentified	18.53	23.28	16.73	20.30	25.11	11.57	16.27		
rodent carcasses	12.13	2.22	14.74	7.92	4.00	24.68	17.50		
sheep	6.50	9.20	2.92	6.34	8.22	5.90	6.71		
grass	1.32	0.78	1.86	1.27	1.11	1.53	1.39		
potatoes	0.54	0.22	0.93	0.54	0.22	0.71	0.54		
wild birds	0.20	0.33	0.13	0.24	0.44	0.00	0.15		
duikers	0.17	0.33	0.00	0.18	0.22	0.12	0.15		
chickens	0.14	0.11	0.00	0.06	0.44	0.12	0.23		
hares	0.14	0.00	0.13	0.06	0.44	0.12	0.23		

proportion of total hunting attempts) also differed between seasons (z = 4.6, d.f. = 1, p < 0.001), but not on sheep (z = 1.5, d.f. = 1, p = 0.2; figure 3).

Among the 491 rodents consumed by AWs, 28% were hunted and 72% were scavenged from traps. AWs exhibited a higher proportion of successful feeding attempts in farmland (36%, n = 229) than in



Figure 3. Probability of African wolves successfully capturing (successful events per total hunting attempts) rodents and sheep during hunting attempts in the wet and dry seasons.



Figure 4. Probability of African wolves successfully capturing rodents in different habitat types.

Table 2. Comparison of African wolves' success in capturing rodents (active hunting) in different habitat types using Tukey multiple comparisons test.

habitat	different	lower	upper	<i>p</i> adj
farmland-bushland	0.197	0.121	0.274	0.0000
grassland—bushland	—0.054	—0.129	0.021	0.212
grassland–farmland	-0.251	-0.335	-0.168	0.0000

bushland (17.3%, n = 324) or grassland (10.7%, n = 244) (figure 4). The proportion of successful feeding attempts did not differ between bushland and grassland (table 2).

During the study period, we observed AWs killing 192 sheep, of which 163 (85%) were killed by solitary AWs, 21 (11%) by pairs and four (2%) by groups of three AWs.

3.2. AW foraging on dead rodents from traps

During the period of barley production (July–November) in 2016 and 2017, 3009 rodents were trapped in *difits* at an average rate of 24.7 ± 8.5 rodents ha⁻¹ d⁻¹ (electronic supplementary material, table S2). The Natal multimammate mouse (*Mastomys natalensis*) was the most frequently captured species in *difits*, accounting for 72.6% of the total. The other four captured species were the Ethiopian white-footed mouse (*Stenocephalemys albipes*, 17.3%), grey-tailed narrow-headed rat (*S. griseicauda*, 5.1%), Abyssinian grass rat (*Arvicanthis abyssinicus*, 4.3%) and *Lophuromys* spp. (0.8%). Eleven rodent species were caught

Table 3. Frequency (%) of rodents and shrews (n = 420) captured in the three zones of GMCCA using Sherman live traps and percentage of rodent species captured in farmland using *difit*. For comparison, frequency (%) of occurrence of rodents per scat (348 scat samples) of EWs in the same study site (data from [11]).

	matrix		buffer		core				
								captured	
species	dry	wet	dry	wet	dry	wet	total	in <i>difit</i>	EW
Arvicanthis abyssinicus	0.2	0.0	0.0	0.0	0.0	0.0	0.2	4.3	59.5
Dendromus lovati	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0	
Lophuromys brevicaudus	0.0	1.0	4.5	14.5	12.4	12.9	45.2	0.8	
Lophuromys flavopunctatus	0.0	0.0	1.4	1.4	0.0	4.0	6.9		
Mastomys natalensis	3.1	0.0	0.0	0.0	0.0	0.0	3.1	72.6	
Otomys typus	0.0	0.5	0.2	1.7	0.0	0.7	4.0	0	25.6
Stenocephalemys albipes	6.0	6.0	0.0	0.0	0.0	0.0	6.0	17.3	
Stenocephalemys albocaudata	0.0	0.0	0.2	6.0	3.3	3.3	17.1	0	
Stenocephalemys griseicauda	2.9	2.9	4.5	2.1	0.0	1.7	11.4	5.1	
Tachyoryctes splendens									30.5
Crocidura baileyi	0.0	0.5	0.0	0.0	0.0	0.5	4.3	0	
Crocidura macmillani	0.0	0.0	0.5	3.1	0.2	0.0	1.4	0	
grand total	12.1	2.14	11.4	29.5	17.4	27.4	100	0	

in Sherman live traps in the study. The Natal multimammate mouse, Ethiopian white-footed mouse and grey-tailed narrow-headed rat were all caught only in farmland (matrix). The remaining species were either captured in the buffer and core zones or in all three zones (table 3).

AWs took most of the rodents from *difit* (81% of events), followed by raptors (*Milvus migrans, Buteo augur:* 12%), caracals (*Caracal caracal:* 2.4%), domestic dogs (2.2%) and domestic cats (1.4%). EWs were observed taking rats in only 1% of *difit* scavenging events.

4. Discussion

This study provides the first detailed observational data on the foraging behaviour of AWs and provides inferences into the extent of dietary overlap with EWs. Earlier scat analyses indicated that rodents comprise a high proportion (47–57%) of the diet of the AW [8,9]. Here, we show that a large proportion (72%; electronic supplementary material, table S1) of the rodents consumed by AWs are obtained via scavenging from traditional traps (*difits*) rather than by hunting. Unlike the rodent specialist EWs [10,12], AWs feed on a greater diversity of food items, including insects, livestock carcasses and live sheep. Surprisingly, arthropods comprised the second most frequently consumed food items by AWs at 19.0%. Given that other sympatric mammals like EWs and gelada monkeys consume insects much less often [11,17], AWs may be unique among large mammals in the Ethiopian Highlands in exploiting a dietary niche in which insects play a major role.

AWs appear to be generally less efficient in capturing live rodents in Afro-alpine habitats (less than 17% success rate) than EWs, which exhibit capture efficiencies between 25 and 66% at Guassa [22] and 45% in the Bale mountains [10]. Whereas active hunting accounted for only 6% of the AW diet, EWs are almost exclusively (greater than 90%, [10]) rodent hunters and seldom scavenge (electronic supplementary material table S1). Thus, AWs exhibit a more omnivorous diet with a prominent scavenging component, whereas EWs are more strict rodent hunting specialists. This difference may be due to EWs preferring intact grassland habitat, and thus not encountering live rodents as frequently as carcasses. Further, the proclivity of AWs for scavenging rodents may reduce the extent of direct exploitative competition between AWs and EWs.

These results highlight the flexible nature of AW foraging behaviour. The foraging behaviour of AWs is highly seasonal and appears to track rodent abundance [8]. Consistent with previous research [8,9], we found that AWs forage on rodents more in the wet season and exploit livestock (sheep) more during the dry season. Indeed, while rodents comprise a large proportion of AW foraging efforts and capture

frequency, active hunting and scavenging of livestock was probably a major, if not the main, component of the diet in terms of biomass. AWs are also more proficient at rodent capture in farmlands compared to more intact habitats (bushland, grassland and woodland) where EWs thrive. The success of AWs in such disturbed habitats may be attributed to the higher visibility of farmland habitats, which evince little above-ground biomass, and/or the nature of rodent abundance and species composition in farmlands [23,24].

The reliance by AWs on rodents and insects implies that they play a role in pest control that may be beneficial to local farmers during certain times of the year [25]. Further, their scavenging of carcasses may have a hygiene benefit around human habitation [26]. Mesocarnivores seem to be on the increase in farm communities worldwide [27,28]. They benefit humans by feeding on crop vermin, and by removing garbage and carcasses, thus reducing health risks [26–28].

The present study points to two conservation recommendations that would facilitate the coexistence of EWs and AWs. First, given the adaptable nature of the foraging ecology of AWs in comparison to EWs, it is crucial that future EW conservation efforts focus on preserving intact habitats that are inherently preferred by EWs. Second, given the extent of persecution of AWs, local farmers should be informed about the potential benefits that AWs have for their farms.

5. Conclusion

This study shows that a large proportion of the rodents whose remains have been found in the scats of AWs were from dead animals caught in traditional traps, rather than obtained through predation, distinguishing them in their foraging habitats from EWs. As a consequence, we may conclude that exploitative food competition between the AW and EW is probably limited. This study also highlights the importance of AWs in rodent control (with their greater efficiency at capturing live rodents in farmland habitats) and waste management (through their removal of rodent and livestock carcasses near farms) in the Ethiopian Highlands. Lastly, it is important to underline that human agricultural expansion into EW habitats is likely attracting AWs, thereby adversely affecting EWs though interference competition [8].

Ethics. Ethiopian Wildlife Conservation Authority (EWCA): Policy for management of wildlife resources guidelines have been followed.

Data accessibility. Data available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.p9g41sd [29].

Authors' contributions. G.T.M., A.A., A.B., C.S.Z. and N.C.S. conceived the study; G.T.M. and M.K. performed the fieldwork; G.T.M, A.A. and D.T. analysed the data and interpreted the results; G.T.M, A.A., V.V.V., P.J.F., D.T. and N.C.S. drafted the manuscript; and C.S.Z., J.M.R., V.V.V., M.K., A.B. and P.J.F. commented on the manuscript and contributed to its final version.

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Tariku Mekonnen Gutema^{1,2}, Anagaw Atickem^{3,4}, Diress Tsegaye^{5,6}, Dessalegn Chala⁷, Afework
Bekele⁴, Claudio Sillero-Zubiri^{8,9}, Jorgelina Marino^{8,9}, Dietmar Zinner³, Vivek V.
Venkataraman¹⁰, Peter J. Fashing^{1,11}, Nils C. Stenseth^{1,4}

7

8 ¹Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences,

9 University of Oslo, PO Box 1066 Blindern, NO-0316 Oslo, Norway

²Department of Natural Resources Management, Jimma University, P.O. Box 307, Ethiopia

¹¹ ³Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research,

12 Kellnerweg 4, 37077 Göttingen, Germany

⁴Department of Zoological Sciences, Addis Ababa University, PO Box 1176, Addis Ababa,

14 Ethiopia

⁵University of Oslo, Department of Biosciences, PO Box 1066 Blindern, 0316 Oslo

⁶Faculty of Environmental Sciences & Natural Resource Management, Norwegian University of

17 Life Science, P.O. Box 5003, 1432 Ås, Norway

18 ⁷Natural History Museum, University of Oslo, Oslo, Norway

19 ⁸Wildlife Conservation Research Unit, Zoology Department, University of Oxford, Tubney

20 House, Tubney OX13 5QL, UK

⁹IUCN SSC Canid Specialist Group, Oxford, UK

¹⁰Institute for Advanced Study in Toulouse, Toulouse France 31000

²³ ¹¹Department of Anthropology and Environmental Studies Program, California State University

24 Fullerton, 800 North State College Boulevard, Fullerton, CA 92834 USA

25 Abstract

26 Recent evidence suggests that the African wolf (Canis lupaster) is a potential competitor of the endangered Ethiopian wolf (C. simensis). Unlike the well-studied Ethiopian wolf, comparatively 27 little is known about the ecology of the African wolf in the Ethiopian highland habitats they share. 28 With the goal of investigating the behavioural ecology of the African wolf, particularly its home 29 range size, habitat use and activity patterns, we studied two populations in the human-dominated 30 landscapes of the northern Ethiopian highlands, Guassa Menz Community Conservation Area 31 (GCCA) and Borena Saynt Worehimenu National Park (BSNP). We followed 11 radio-collared 32 African wolves (5 in GCCA, 6 in BSNP) for 16 months (659 ± 83 sightings for each individual). 33 The mean 95% kernel density estimate home range size of African wolves in BSNP was more than 34 twice that of conspecifics in GCCA ($4.5 + 1.5 \text{ km}^2$ versus $2.2 + 0.7 \text{ km}^2$). AWs were solitarily in 35 55% of total sightings (n=3,934) and in groups of 2 to 7 during the other 45% (n=3,291). Further, 36 37 at both sites, individuals preferred areas in proximity to human settlements and were active mainly at dawn and dusk. The study provides the basic knowledge on spatial and temporal ecology of 38 African wolf that will help us to understand the extent of resource partitioning with Ethiopian 39 wolves. On the other hand, the significant variation in home range size in different habitats may 40 illustrate the plasticity of African wolves and their ability to respond to human-induced landscape 41 changes which might give African wolves a competitive edge over Ethiopian wolves. 42

43

44 Keywords: Canis lupaster, Canis simensis, Ethiopian highlands

46 Introduction

The African wolf (AW) occurs in parts of northern and eastern Africa including Ethiopia (Rueness *et al.*, 2011; Gaubert et al., 2012; Moehlman & Jhala, 2013). In the Afroalpine habitats of the Ethiopian highlands, AWs are often found in sympatry with the endangered Ethiopian wolf (EW), *Canis simensis* (Atickem et al., 2017). In contrast to the well-studied EW, little information on the behaviour, ecology and conservation status of AWs in Ethiopia is available, 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).

We studied the foraging ecology of AWs at two broadly similar sites in the Ethiopian 54 55 highlands, Guassa Menz Community Conservation Area (GCCA) and Borena-Saynt National Park (BSNP) (Gutema et al., 2019), focusing particularly on the potential for interspecific competition 56 between AWs and EWs in GCCA (Gutema et al., 2018a). Interactions between the two-canid 57 58 species are typically agonistic and characterized by site-specific dominance, though the number of individuals of each species present during an encounter sometimes influences outcomes as well 59 (Gutema et al., 2018a). AWs also tend to occupy more anthropogenically-modified habitats and 60 consume more diverse diets than EWs which are rodent specialists and prefer ecologically-intact 61 habitats (Ashenafi et al. 2005; Gutema et al., 2018a; Marino 2003; Marino, et al. 2010). 62

Here we expand our ecological research on AWs by determining home-range size, habitat 63 use, and activity patterns at GCCA and BSNP, both areas consisting largely of Afroalpine 64 grassland habitat bordered by farmland. The home range sizes of adult AWs (n=3) in and adjacent 65 to the Bale Mountains National Park in southern Ethiopia have been found to vary between 8 and 66 48 km² (100% minimum convex polygon) and do not overlap with the ranges of EWs (Admasu et 67 al. 2004). This is the largest home range size recorded for AWs in other part of Africa, which are 68 less than 20km² 100% MCP (Fuller et al., 1989; Sillero Zubri and Macdonald, 1994). However, to 69 provide a more complete insight into AWs home range and activity pattern, further research on 70

spatial and temporal habitat use in areas with different in anthropogenic impacts and EWspopulation is needed.

Habitat use by wolves and jackals varies considerably between different areas, based not 73 only on habitat availability but also on the presence or absence of other species of canids (Kingdon, 74 1977; Loveridge and Macdonald, 2002). For instance, in the areas where AWs are sympatric with 75 Black backed jackals Canis mesomelas and Striped jackals Canis adusta, AWs uses dry open 76 grassland (Kingdon 1977) while C. mesomelas uses open woodland (Fuller et al. 1989) and C. 77 adusta uses more densely vegetated habitats (Fuller et al. 1989; Kingdon 1977). Furthermore, the 78 peak activity time for AWs was during a day, while C. adusta was more active during night and 79 80 C. mesomelas at dawn (Fuller et al. 1989). These studies suggest that co-existence between the species is promoted through both spatial and temporal niche partitioning. 81

With our study, we aim to provide more data from two protected areas in northern highlandsof Ethiopia on home-range size, habitat use and activity pattern of AWs.

84

85 Methods

86 Study area

The study was carried out in Guassa Menz Community Conservation Area (GCCA) and Borena 87 Saynt Worehimenu National Park (BSNP), which are located in north central Ethiopia (Fig. 1). 88 GCCA covers an area of 111 km² and consists mainly of Afroalpine grassland and *Erica* 89 moorlands, protected by the local community for the past 400 years (Ashenafi et al., 2005). We 90 focused our study on the southern part of the GCCA where AWs and EWs are sympatric and 91 agonistic interactions between the species are common (Gutema et al., 2018a). The BSNP 92 comprises 153 km² at elevations from 1.900 - 3.700 m and has been protected as a National Park 93 94 since 2001 (Eshete et al., 2018). At BSNP, we collared AWs in the western part of the protected area where EWs were rarely observed during our study. Instead, EWs seemed to be concentrated 95 in the eastern BSNP where we did not conduct research. According to Marino and Sillero-Zubiri 96

97 (2011), the total number of adult EWs have been 23 in GCCA and 16 in BSNP, while the largest
98 population of EWs are in BMNP (around 250 individuals).

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 \pm 243 mm per year, 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 mammals endemic to Ethiopia including Ethiopian 105 106 wolves, gelada monkeys (Theropithecus gelada) and Starck's hare (Lepus starcki): Lophuromys, Crocidura, Arvicanthis and Stenocephalemys spp are among the small mammals recorded in both 107 areas (Gutema, 2019). Lophuromys are the most abundant small mammals in both GCCA (52%, 108 109 relative abundance) and BSNP (54% relative abundance) (Chane and Yirga, 2014; Eshete et al., 2018; Gutema et al. 2018a). Both study sites are bounded by villages and agriculture where people 110 rely economically on barley and livestock production (especially sheep and goats), providing 111 similar anthropogenic food resources for AWs (Gutema et al. 2019). 112

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

120







124 Figure 1. Study localities, Guassa-Menz Community Conservation Area (GCCA) and Borena

- 125 Saynt Worehimenu National Park (BSNP)
- 126 Trapping and collaring

127 Fourteen AWs (seven in GCCA and seven in BSNP) from eight packs (four packs from each site)

128 were captured using rubber padded leg hold traps and fitted with very high frequency (VHF)

129 collars (for detailed procedures of the capture and collaring see Gutema et al, 2018b).

130 Data collection

During 2016 and 2017, focal observations were carried out on 11 of the 14 collared AWs (six in BSNP and five in GCCA) and their location was recorded at 30 min intervals from distances of 50-150 m. When visual contact was not possible (particularly at night), tracking accuracy was determined by hiding a transmitter (collar) in an undisclosed position, enabling comparison between actual and estimated positions (Loveridge and Macdonald, 2002). During focal follows, habitat type (bushland, grassland, farmland and woodland) and group size were also recorded at 30' interval when possible. Data from three collared individuals were excluded from the analysis
due to the low number of locations recorded for each. Two were found dead, possibly killed byhumans, and the signal lost for the other after only three months (Gutema et al. 2018a).

140 The number of individual AWs in each pack (group size) was determined during tracking.

141

142 Home range estimates

Home ranges were estimated for each radio-collared individual using the minimum convex 143 polygon (MCP) and fixed kernel density estimation (KDE) techniques. MCP estimates are 144 presented to enable comparison with most previous studies (Admasu et al. 2004). However, this 145 method has been widely criticized in that it often overestimates home range size (Worton 1989). 146 147 Therefore, home ranges were also calculated using KDE, which is now generally regarded as the most accurate estimator of home range size (Wauters et al, 2007). KDE is a parametric technique 148 for estimating home range size that allows identification of distinct (core) areas of activity, which 149 150 can be an especially important consideration in areas where habitats have been fragmented. We used 95% of all points to estimate the KDE home range size and 50% kernel home range was used 151 as an estimate of core area. 152

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154 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 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). 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).

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163 Activities and group size

Activities of the focal wolf were recorded as 'travelling' (moving without hunting or feeding), 164 'resting' (sleeping, sitting, 'hunting' (attempting to capture prey), 'feeding' (ingesting prey or 165 other food) and 'social interaction' (playing, greeting, grooming, group howling) (Leuchtenberger 166 et al., 2018). To determine activity peaks, we divided activities into two categories inactive 167 (resting) and active (all other behaviours). For this analysis, the 24-hour cycle was divided into 168 four discrete periods, 04:01-10:00 h (dawn-morning), 10:01-16:00h (midday), 16:01-22:00h 169 (dusk-evening), 22:01–04:00 h (mid night) (Leuchtenberger et al. 2018). Number of conspecifics 170 nearby was also recorded. We considered animals to be in a group when they were <50 m from 171 one another. 172

173

174 Data analysis

We produced a 100% MCP and 95% KDE home range size as well as a 50% KDE core area size 175 176 for each collared individual at each site. 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 177 two levels (i.e. BSNP and GCCA), considering each individual as the sampling unit, and home 178 range size as the response variable. We compared habitat preferences using general linear models 179 for each site separately. In this model, habitat type with four levels (farmland, grassland, bushland 180 and woodland) and daytime with two levels (day and night) were used as fixed effect factors and 181 individual collared animals as random effects. We estimated percentage time spent per hour in 182 relation to activity with two levels (active and resting) and time (i.e. 24-hours cycle) using a 183 general linear model. All analyses were carried out in R version 3.5.1 (R Core Team 2018). 184

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190 **Results**

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192 Home range

- 193 We recorded 8244 AW locations (BSNP: n=4078; GCCA: n=3169) between April 2015 and
- 194 November 2017 (for details on each individual see Table S1). The mean + SD 95% KDE home
- range size of AWs was twice as high $(4.5 \pm 1.5 \text{ km}^2)$ at BSNP and than at GCCA $(2.2 \pm 0.7 \text{ km}^2)$
- 196 (Table 1; Fig.3). The 50% KDE the core area sizes were also higher at BSNP (0.59 ± 0.17) km²)

than at GCCA (0.38 ± 0.10). Home range size varied significantly between the two sites for both

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198 the 95% (F= 10.12, df = 9, P= 0.01) and 50% KDE (F= 6.614, df = 9, P= 0.03; Table S2).
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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 were estimated using the 100% minimum convex polygon (MCP) and 95% and 50% fixed kernel density estimation (KDE) techniques.

Study site	Individual	Age	Sex	# of	50%	95%	100% MCP
	ID			locations	KDE	KDE	
BSNP	Anm350	Adult	Female	787	0.49	3.17	10.7
	Anm370	Adult	Male	816	0.52	2.26	6.63
	Anm390	Adult	Male	643	0.68	5.75	15.40
	Anm470	Adult	Female	661	0.73	4.76	19.77
	Anm430	Subadult	Male	545	0.35	5.70	12.57
	Anm510	Subadult	Female	623	0.78	5.33	16.01
GCCA	Anm290	Adult	Male	656	0.35	2.68	12.39
	Anm310	Adult	Male	564	0.46	2.64	5.17
	Anm450	Subadult	Female	676	0.27	1.46	9.16
	Anm490	Adult	Female	603	0.49	2.85	5.31
	Anm550	Adult	Female	670	0.31	1.58	9.73



Figure 3: Comparison of mean <u>+</u> SD 95% and 50% kernel density estimate (KDE) home range
sizes (km²) of African wolves in Borena Saynt National Park (BSNP, grey boxes, n=6) and Guass
Menz Community Conservation Area (GCCA, yellow boxes, n=5).

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205

210 Hbitat use

Patterns of habitat use were inferred from 3919 diurnal 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 in 6% in the core. Conversely, in GCCA (of 3170 observation), 57%41% of AW of AW sightings were in the buffer, 41% in the matrix, and 2% in the core.



Figure 4: Distribution of the study individuals of AWs in Borena Saynt Worehimenu National



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. 5; Table S2).



Figure 5: 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).

228

229 Activities and group size

Frequency of occurrence of each activity type varied across time at both sites (Fig. 5). Although AWs were active during both day and night, their peaks in activity were between 04:00 and10:00 (dawn-morning) and 16:00-20:00 (dusk-evening) (Fig. 6). 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 S3).

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Figure 6. Percentage of active time (travelling, foraging 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).

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AWs were solitarily in 55% of total sightings (n=3,934) and in groups of 2 to 7 during the other 45% (n=3,291) (Table 4). AWs were usually observed alone during the daytime and in groups at night (Fig. 7). AWs were more often found in groups at GCCA than at BSNP (Table S4; Table S5). In particular, of diurnal AW sightings, 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).



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Figure 7. Total counts of African wolf individuals recorded during focal follows of 11 collared
African wolves at BSNP (n=6) and GCCA (n=5).

251

252 **Discussion**

This study addressed the ranging, habitat use, and activity patterns of AWs at two sites in theEthiopian Highlands. First, our study shows that the home ranges size of AWs varies across the

study sites. The home range size of AW populations in BSNP was more than twice that of the 255 populations in GCCA (4.5 versus 2.2 km² 95% KDE). Remarkably, in areas adjacent to Bale 256 Mountains National Park, the average 100% MCP home range size estimate for AWs was four 257 times larger (32km²; Admasu *et al.*, 2004) than that estimated in our study in GCCA (8.4km² 100%) 258 MCP). From the studies in Serengeti, the defended territory of AWs, ranges between 1 and 3 km² 259 (at 95% KDE, Moehlman, 1986; Creel and Creel, 2002). This significant variation in home range 260 size illustrates the plasticity of AWs space use, which may enhance the ability of AWs to respond 261 to human-induced landscape changes. This might contribute for dominance of AWs over EWs in 262 interference competition with the recently increasing human induced habitat disturbance (habitat 263 264 loss and fragmentation due to agriculture and overgrazing) in Ethiopian Highlands. Habitat fragmentation, prey distribution, body mass and interspecific competition are among the major 265 factors that affect home range size (Erlinge et al., 1990; Mysterud et al., 2001; Caro and Stoner, 266 267 2003; Hayes et al., 2007; Ofstad et al., 2016). Similarly, the home range sizes of red foxes (Vulpes vulpes) ranges from 2.4 km² to 358km² (MCP100%) that show their plasticity to landscape 268 changes (Walton, et al., 2017). 269

In both study areas, AWs are known to prefer area in proximity to human habitats. Thismight be explained by the lower rodent hunting efficiency of AWs in Afroalpine

habitat compared to EWs (Gutema et al., 2019) and abundance of anthropogenic resources 272 around human settlement. However, relatively more AWs were recorded in core zone in BSNP 273 (6% of the total locations recorded, n=4076) compared to GCCA (2%, n=3170) which might be 274 the impact of interspecific competition with EWs in GCCA. Admasu et al. (2004), from the study 275 of seven collared AWs in and adjacent to Bale Mountains National Park, investigated that AWs 276 are restricted to the mosaic of farmland, grassland and woodland of the edge and adjacent to the 277 Park and do not overlap with EWs. This might be explained by the dominance of EWs due their 278 high population in the park (estimate total population= 250 individuals; Marino and Sillero-Zubiri, 279 2011). Similarly, black-backed jackals (Canis mesomelas) in South Africa prefers areas near to 280

human settlement (Humphries et al., 2016). So need a better concluding sentence about what your
results mean in relation to these others.

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

Our study shows that AWs are mainly crepuscular (active at dawn and dusk) but they were 289 290 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 early morning and late 291 afternoon (Kaunda, 2001). On the other hand, the sympatric EW is active mainly during the day 292 293 (diurnal) due to their major diets, diurnal rodents (Sillero-Zubiri and Gottelli 1995, Ashenafi et al., 2005; Sillero-Zubiri et al., 2004; Eshete et al., 2018). This is mechanism of reducing direct 294 interspecific competition by exploiting the same area at different time of day (Loveridge and 295 Macdonald, 2003; Rechetelo et al., 2016; Machado et al., 2017). The AWs in GCCA spent a higher 296 proportion of time resting (27%, n=2,979) than the AWs in BSNP (16%, n=4,035). This might be 297 due to the interference competition with EWs that exclude them to use the intact habitat during a 298 daytime and human activities in buffer zone. 299

AWs were observed in groups more often in GCCA than in BSNP (Table S4). This might be due to the interference competition with EWs, in that the likelihood of AWs winning agonistic interactions increased with group size (Gutema et al., 2018a).

In summary, the study revealed the AW's flexibility in home range size that show ability to respond 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 major causes of spatial and
temporal niche partitioning of AWs and EWs in Ethiopian highlands

314

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320 collaring of AW for this study

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- 436 Supplementary
- Table S1. Percentage of sightings of each African wolf in the study (n=11) alone or in groups of
- 438 different sizes at Borena-Saynt National Park (n=6) and Guassa Community Conservation Area

439 (n=5).

ID		1			2			3			4			5		N
	d	n	sum	d	n	sum	d	n	sum	d	n	sum	d	n	su	
															m	
BAnm310	32.6	15.1	47.7	15.6	26.6	42.2	3.6	4.4	8.0	1.6	0.5	2.1	0.0	0.0	0.0	564
BAnm350	41.4	18.5	59.8	14.1	18.7	32.8	1.9	4.7	6.6	0.4	0.3	0.6	0.0	0.1	0.1	786
BAnm370	32.6	30.1	62.9	15.2	12.9	28.1	2.0	6.5	8.5	0.0	0.5	0.5	0.0	0.0	0.0	815
BAnm430	46.2	25.1	71.2	9.7	10.1	19.8	2.4	4.5	7.3	0.6	0.8	1.3	0.0	0.4	0.4	535
BAnm450	29.9	9.8	39.7	16.0	20.2	36.2	6.8	12.7	19.6	1.8	2.5	4.3	0.3	0.0	0.3	675
BAnm470	40.6	23.9	64.5	9.0	15.5	24.5	4.0	5.8	9.7	0.6	0.2	0.8	0.2	0.3	0.5	657
GAnm290	31.4	14.5	45.9	11.6	20.7	32.3	6.7	10.4	17.1	2.9	1.2	4.1	0.3	0.3	0.6	656
GAnm390	39.0	27.7	66.7	9.3	15.6	24.9	2.5	4.5	7.0	0.3	0.9	1.2	0.0	0.2	0.2	643
GAnm490	24.9	12.5	37.4	26.6	26.1	52.7	5.8	3.2	9.0	0.5	0.5	1.0	0.0	0.0	0.0	602
GAnm510	41.7	23.8	65.5	9.5	12.1	21.6	4.8	6.1	11.0	0.6	1.0	1.6	0.2	0.2	0.3	621
GAnm550	30.6	15.7	46.1	11.6	21.9	33.5	6.9	9.4	16.2	1.6	2.2	3.9	0.0	0.2	0.2	671
Mean%	35.5	19.9	55.3	13.5	18.1	31.6	4.3	6.7	10.9	1.0	1.0	1.9	0.1	0.1	0.2	7225

440 d = day, n = night

441

- Table S2 Statistical comparison of (a) 95% and (b) 50% KDE home range sizes for African wolves
- 443 at BSNP and GCCA.

444 a) KDE 95%

Coefficients:	Estimate	Std.Error	t value	Pr(> t)
(Intercept)	4.4950	0.4776	9.413	5.91e-06 ***
SiteGCCA	-2.2530	0.7083	-3.181	0.0112 *

445

448

449 b) KDE 50%

Coefficients:	Estimate	Std. Error	t value	$Pr(\geq t)$
(Intercept)	0.59167	0.05654	10.465	2.45e-06 ***
SiteGCCA	-0.21567	N0.08386	-2.572	0.0301 *

450

451 Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

453

⁴⁴⁶ Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

⁴⁴⁷ F-statistic: 10.12 on 1 and 9 DF, p-value: 0.01117

⁴⁵² F-statistic: 6.614 on 1 and 9 DF, p-value: 0.0301

Table S3 Analysis of African wolves habitat use patterns at Borena-Saynt National Park (BSNP),

Guassa Menz Community Conservation Area (GCCA).

BSNP

Coefficients:	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	12.333	3.317	3.718	0.000615 ***
Habitat-Grassland	26.000	4.691	5.543	2.08e-06 ***
Habitat-Bushland	35.000	4.691	7.461	4.31e-09 ***
Habitat-Woodland	-10.833	4.691	-2.309	0.026167 *
Habitat-Grassland: Day-Night	-36.333	6.634	-5.477	2.57e-06 ***
HabitatBushland:Day-Night	-68.833	6.634	-10.376	6.60e-13 ***
HabitatWoodland:Day-Night	-36.833	6.634	-5.552	2.01e-06 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' 1 GCCA

459 460

Coefficient	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	12.200	3.819	3.195	0.00314 **
Habitat-Grassland	5.400	5.400	1.000	0.32485
Habitat-Bushland	44.400	5.400	8.222	2.16e-09***
Habitat-Woodland	1.200	5.400	0.222	0.82557
Habitat-Grassland:Day-Night	-7.600	7.637	0.995	0.32715
Habitat-Bushland: Day-Night	-43.000	7.637	-5.63	3.17e-06***
Habitat-Woodland:Day-Night	-25.200	7.637	-3.300	0.00238 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table S4. Percentage of time devoted to different activities by African wolves at BSNP and GCCA

466 during four 6-hour time intervals.

Time intval	04:01-10:00		10:01-16:00		16:01-22:00		22:01-04:00		overall	
site	GCCA	BSNP	GCCA	BSNP	GCCA	BSNP	GCCA	BSNP	GCCA	BSNP
n	816	1286	769	900	848	1171	546	678	2979	4035
feed	37.6	20.0	12.6	10.3	24.7	19.1	13.2	10.2	20.4	15.9
hunt	23.4	34.3	16.3	21.2	33.7	23.6	15.1	20.2	25.2	25.9
rest	18.2	9.1	31.7	26.5	11.6	10.8	46.5	26.9	28.3	16.5
travel	20.8	36.6	39.5	41.9	30.0	46.5	25.2	42.7	26.2	41.7

467

- 468 Table S5. Frequency of observed group sizes of African wolves (% of observations) at Borena
- 469 Saynt Worehimenu National Park (BSNP) and Guassa Menz Coomuunity Conservation Area
- 470 (GCCA) during the day versus night.

Group size	BSNP day	BSNP night	GCCA day	GCCA night
	n=2222	n=1854	n=1707	n=1663
1	72.9	51.0	55.6	32.3
2	21.0	23.5	30.0	44.3
3	5.3	5.9	11.0	19.8
>4	1.0	1.0	1.0	3.5

IV

African wolf diet, predation on livestock and conflict in the Guassa mountains of Ethiopia

Anagaw Atickem^{1,2,3}*, Getachew Simeneh², Afework Bekele², Tariku Mekonnen¹, Claudio Sillero-Zubiri^{4,5}, Russell A. Hill⁶ and Nils Chr. Stenseth^{1,2}

¹Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, NO-0316, Oslo, Norway, ²Department of Zoological Sciences, Addis Ababa University, P. O. Box 1176, Addis Ababa, Ethiopia, ³Cognitive Ethology Laboratory, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany, ⁴Wildlife Conservation Research Unit, Zoology Department, University of Oxford, The Recanati-Kaplan centre, Tubney house, Tubney OX13 5QL, U.K., ⁵IUCN/SSC Canid Specialist Group, The Recanati-Kaplan centre, Tubney house,Tubney OX13 5QL, Oxford, U.K. and ⁶Department of Anthropology, Durham University, Dawson Building, South Road, Durham DH1 3LE, U.K

Abstract

The African wolf (Canis lupus lupaster) was first identified in 2011 in the Ethiopian highlands, with its status as a new species confirmed in 2015. We studied the diet of a confirmed African wolf population in the Menz-Guassa Community Conservation Area of central Ethiopia from scat samples collected by den sites from August to November 2010. Rodents were found to be the principal food items occurring in 88.1% of scats (n = 101), followed by plant material (34.7%) and insects (21.8%). Information on reported livestock predation and ensuing conflict with the agro-pastoral community was obtained through a questionnaire survey. Interview respondents listed the African wolf as the most serious predator of livestock, accounting for 74.6% of the reported kills (n = 492) and 78.9% of the economic loss. Over 70% of reported livestock predation occurred during the dry season (January-April). Better livestock management during this period may significantly reduce conflict. As sympatric Ethiopian wolves primarily feed on rodents, further studies on the foraging ecology, niche overlap and interspecific interactions between the two species should be studied to determine the extent of competition between the two species.

Key words: African wolf, diet, exploitative competition, golden jackal, human–carnivore conflict

Résumé

Le loup africain (*Canis lupus lupaster*) a été identifié pour la première fois en 2011 sur les hauts-plateaux éthiopiens et

son statut de nouvelle espèce a été confirmé en 2015. Nous avons étudié le régime alimentaire d'une population reconnue comme étant de loups africains dans l'Aire de Conservation communautaire de Menz-Guassa, au centre de l'Éthiopie, à partir d'échantillons de crottes récoltés près des tanières entre août et novembre 2010. Nous avons découvert que les rongeurs constituaient l'aliment principal, présents dans 88,1% des crottes (n = 101), suivis par des matières végétales (34,7%) et des insectes (21,8%). Nous avons recueilli des informations sur la prédation de bétail et sur les conflits qu'elle cause avec la communauté agro-pastorale au moyen d'une enquête par questionnaire. Les participants classaient le loup africain comme le plus sérieux prédateur du bétail, comptant pour 74,6% des rapports d'animaux morts (n = 492) et pour 78,9% des pertes économiques. Plus de 70% de la prédation de bétail rapportée se passait durant la saison sèche (janvier-avril). Une meilleure gestion du bétail pendant cette saison pourrait réduire significativement les conflits. Étant donné que les loups d'Abyssinie, sympatriques, se nourrissent principalement de rongeurs, il faudrait faire de nouvelles études sur l'écologie alimentaire, le recouvrement des niches et les interactions interspécifiques pour déterminer l'étendue de la compétition entre ces deux espèces.

Introduction

The African wolf (*Canis lupus lupaster*) was first reported in the Ethiopian highlands from evidence of mitochondrial haplotypes in 2010 (Rueness *et al.*, 2011). A recent genomewide sequencing confirmed its unique species

^{*}Correspondence: E-mail: anagawam@gmail.com

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status (Koepfli et al., 2015; Rueness et al., 2015). The African wolf was formerly confused with golden jackal (Canis aureus), which was once considered as a monophyletic species widely distributed throughout the Middle East, south-eastern Europe and Asia (Wayne et al., 1997; Jhala & Moehlman, 2008; Rueness et al., 2011). Koepfli et al. (2015) proposed that the entire African golden jackal group belonged to the same African wolf species, while Gaubert et al. (2012) suggested the possibility of both African wolf and African golden jackal co-occurring in Africa. So far, the African wolf has been confirmed in several African countries including Ethiopia and Egypt (Rueness et al., 2011), Algeria, Mali and Senegal (Gaubert et al., 2012), Kenya (Koepfli et al., 2015) and Morocco (Waters et al., 2015). Nevertheless, reliable population estimates are largely absent and little information is available on its conservation status (it is not yet listed under the IUCN Red List of Threatened Species).

Large carnivores are experiencing massive declines in their populations and geographic ranges around the world due persecution by humans, mainly as a result of conflict over perceived and actual livestock predation (Ripple et al., 2014). The extermination of the Mexican wolf (Canis lupus *baileyi*) from its entire natural range by the 1970s (Brown, 1983), decimation of grey wolves in most areas of the United States by the mid-1930s (Mech, 1995) and the extinction of the Falkland wolf (Dusicyon australis) in 1876 (Sillero-Zubiri, 2015) as a result of livestock predation are some examples. During the last two decades, efforts have been made to reintroduce grey wolves in the United States, both to conserve the species but also to restore and maintain healthy wildlife communities (Bangs et al., 1998; Nilsen et al., 2007). Yet, the degree of the humancarnivore conflict is escalating as humans further convert land for their activities and displace or exploit herbivores and so reduce the availability of wild prey to carnivores (Thirgood et al., 2000; Treves & Karanth, 2003; Graham, Beckerman & Thirgood, 2005; Lyamuya et al., 2014). Understanding patterns of diet selection and the levels of perceived and actual livestock predation is thus important to developing effective conservation management plans and designing appropriate measures to reduce livestock loss (Sekhar, 1998; Ogada et al., 2003; Wang & Macdonald, 2006; Constant, Bell & Hill, 2015). This is particularly important for species where little other information exists on their status and conservation.

Competition between members of the different carnivore species may lead to declines or extinction of species of conservation concern. For example, the decline in grey wolf numbers in Italy is thought to be partially due to competition with stray dogs (Boitani, 1992). Similarly, the dingo (*Canis lupus dingo*) may have displaced by exploitative competition both the thylacine (*Thylacinus cynocephalus*) and the Tasmanian devil (*Sarcophilus harrisi*; Lever, 1994). African wild dog (*Lycaon pictus*) populations may be limited by the presence of larger carnivores (Creel & Creel, 1996).

The presence of the African wolf has been confirmed throughout the Ethiopian highlands where it overlaps the much more restricted range of the Ethiopian wolf (Canis simensis) (Atickem et al., unpublished; Marino, 2003; Marino & Sillero-Zubiri, 2011). Hence, understanding the behavioural ecology of the African wolf is important not only to develop a conservation management plan for the species itself, but also because of its potential effects on the survival of the IUCN Endangered Ethiopian wolf. Depending on the degree of overlap on diet and habitat selection, African wolves could potentially affect the survival of Ethiopian wolves through exploitation and/or interference competition (Rosenzweig, 2000). As the Ethiopian wolf has a small population of <500 individuals restricted to the Afroalpine ecosystem of the Ethiopian highlands (Marino & Sillero-Zubiri, 2011), such impacts could be very significant.

We studied the diet of African wolves to provide baseline natural history information, investigate the importance of livestock in their diet and examine potential for competition with Ethiopian wolves. We also studied the level of livestock predation by both species and other carnivores in the Guassa Mountains of Ethiopia to assist with the development of conservation management plans for the region.

Methods

Study area

The study was carried out in the Menz-Guassa Community Conservation Area of northwest Shewa, Ethiopia, an area of 111 km² ranging in altitude from 3200 to 3700 m asl (Ashenafi *et al.*, 2005; Fig. 1). Mean annual rainfall was 1650 (\pm 243) mm per year, with more than half falling during the wet season (July and August: Fashing *et al.*, 2014). The dry season was November to February. The vegetation cover in particular grassland is totally degraded during late dry season (January and February). Guassa is a



Fig 1 Study area in the central highlands of Ethiopia, Menz-Guassa Community Conservation Area

centre of endemism for Ethiopian mammals including Ethiopian wolf and gelada *Theropithecus gelada* (Venkataraman *et al.*, 2015). The Ethiopian wolf population in Menz-Guassa was estimated at 21 individuals in 2000 (Ashenafi *et al.*, 2005) and 23 individuals in 2010 (Marino *et al.*, 2011). During this study, five groups of African wolf were identified in the Guassa area with a total population size estimated at seventeen individuals.

Diet

The diet of the African wolf was studied from scat samples collected between October and December 2010. To avoid confusion with scats of other canids, samples were collected from den sites of the African wolf in areas where Ethiopian wolf and domestic dogs were not observed throughout the study period. Five den sites were identified by following African wolf individuals during the first 6 weeks of the study period with information from sheepherders used to identify initial African wolf locations. All den sites were in the periphery of the park and were dominated by bushland. The Ethiopian wolf inhabits the central grasslands and was not recorded near those den sites. Unlike the Bale Mountains, where domestic dogs sometimes follow shepherds (Atickem et al., 2010), we did not see any dogs out of the villages either with humans or alone.

Scat samples were sun dried and broken to pieces to distinguish plant materials intact. The samples were then ground in a mortar and washed in a 1-mm sieve using hot water to separate prey components and other indigestible remains (Mbizah, Marino & Groom, 2012). Finally, each component was identified assisted by magnifying instruments and reference specimens collected from Guassa Mountains and collections at Addis Ababa University. Rodent species were identified from their teeth patterns. Diet analysis was carried out based on the frequency of occurrence per scat as the percentage of scats containing a particular food item (Breuer, 2005; Klare, Kamler & Macdonald, 2011).

Human-carnivore conflict

The level of human African wolf conflict was assessed based on a questionnaire survey of 250 randomly selected households that bordered the park in the vicinity of the range of the African wolf and Ethiopian wolf during October 2010. Every second, households at the buffer zone of the protected area were sampled and no residents declined to be interviewed. From the total respondents, 180 were males and 70 were females; all were adults aged above 18 years, but they varied in their educational level (Table S1). The questionnaire focused on whether the family lost livestock due to carnivore predation during the last 3 years, and if yes, further questions were asked on which livestock species was predated, the responsible carnivore (Ethiopian wolf, African wolf, spotted hyaenas Crocuta crocuta and serval Leptailurus serval) and the time of day and season predation occurred. Community members in the Ethiopian highlands had considerable knowledge of the predators living in their vicinity and were able to reliably identify the predators responsible (Atickem et al., 2010). As sheep and goats were nearly always attended by shepherds during the day, who may then kill the carnivore responsible, the diurnal predators were often confirmed from remains of the kills. African wolf and Ethiopian wolf kill sheep only during daytime. Spotted hyaenas kill at night, and so were inferred from nocturnal losses. The economic losses to African wolf and Ethiopian wolf were then estimated using average local prices of sheep and goat during 2010 (\$19.80 and \$13.80, respectively).

Households were also asked how they attempted to reduce livestock predation through a questionnaire survey (with options of guarding more attentively, moving their sheep grazing system away from the African wolf habitat, reduction in sheep number and attacking wolves to minimize their number). The attitude of the respondents towards African wolf and Ethiopian wolf (positive, negative or neutral) was also questioned during the survey. The livestock shelter used by the local community during the night was recorded, and the number of livestock in each of the 250 households was counted during the early morning before the livestock were let out.

Killing of African wolves during their breeding season by blocking den sites was reported during the survey. To confirm these allegations, we monitored three African wolf groups using VHF collars (Telemetry Solutions, Concord, CA, U.S.A.). Den sites of the collared individuals were then monitored during March–April 2010 to record the potential activities of local community in blocking the den sites.

Results

A total of 101 African wolf scats were collected from five den sites. Rodents (*Arvicanthis abyssinicus* and *Lophuromys flavopunctatus*) were the most frequently occurring food item, present in 88.1% of scats (Table 1).

Table 1 Frequency occurrence of food items in 101 scats

Item	% Frequency of occurrence
Rodents Arvicanthis	88.1
and Lophuromys spp.	
Sheep	2
Bird feathers	2
Insect	21.8
Leaves of crops and grass	31.7
Vegetable	3
Plastic materials	5.9

Table	2	Numbe	er of	livestocl	c predated	over	3-year	period	
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A total of 492 domestic livestock were reportedly killed by carnivores by the 250 households in the 3 years prior to the study (Table 2). There is a significant difference on the number of livestock species kept by the local community ($X^2 = 1533.65$, d.f. = 4, P < 0.001). Sheep, the most abundant livestock in Guassa area comprising 60% of the livestock population, were the most common quarry, accounting for over 90% of reported events. Goats accounted for a further 7%. Large livestock species (i.e. donkeys, horses and cattle) constituted <2% of the total livestock losses reported, primarily killed by spotted hyaenas.

African wolves, generally identified by shepherds following attacks on their sheep during the day, were responsible for 75% of the losses. Of these, 79% of the predation took place between 11:00 and 15:00 hours. Ethiopian wolves were the second most reported predator, accounting for 21% of losses, with servals contributing <1%, usually taking lambs and goat kids. Spotted hyaenas accounted for 5% of reported kills, almost all during the night and on livestock found outside shelters. Overall, African wolves accounted for significantly more predation events ($X^2 = 690.28$, d.f. = 3, P < 0.001). A significant difference was also observed on the predation of small livestock (sheep and goat) by Ethiopian wolf and African wolf ($X^2 = 151.19$, d.f. = 1, P < 0.001). No hyaena kills were reported from inside livestock shelters (96% of households kept their livestock in stone-walled shelters during the night).

Predation was more intense between January and April, peaking in March, with over 70% of kills occurring during this period (Fig. 2). This coincided with the birth of African wolves' pups. The three monitored groups gave birth to

Livestock	% Livestock from 2010 estimate from total 4342 livestock	Mean livestock holding/ household	Carnivore predation events reported over 3-year period				
			African wolf	Ethiopian wolf	Serval cat	Hyaena	Total
Sheep	59.7	10.4 ± 2.8	351	83	0	11	445
Goat	7.8	1.4 ± 0.6	16	18	1	0	35
Cattle	18.4	3.2 ± 1.2	0	0	0	1	1
Donkey	9.4	1.6 ± 1	0	0	0	8	8
Mule	2.4	0.4 ± 0.5	0	0	0	0	0
Horse	2.4	0.4 ± 0.5	0	0	0	3	3
Total	100	_	367	101	1	23	492

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Fig 2 Livestock depredation rate across different months of the year $% \left({{{\left[{{{{\bf{F}}_{{\bf{F}}}} \right]}_{{{\bf{F}}_{{{\bf{F}}}}}}} \right)} \right)$

three to five pups between February and April, with the two collared groups changing den sites five to seven times during this period as they were blocked by the local people. From the twelve den sites used by the three African wolf groups, eight were found blocked by local people. While killing of adult African wolf is not easy, pups are more vulnerable, because they can be blocked in a den using rocks.

Over 11% of the households' total livestock holdings were reported lost to predators during the 3 years prior to the study. African wolf predation on sheep equated to approximately 0.49 sheep per household per year, while the Ethiopian wolf contributed 0.13 loses per year in each household. Collectively this equated to about \$8151 of lost revenue due to predation by African wolf and Ethiopian wolf on sheep and goat in the region, approximately \$10.9 per year per household. African wolves contributed 78.9% of the total economic loss.

While 85.2% of respondents had positive attitudes towards the Ethiopian wolf, only 19.2% of respondents had positive attitudes towards the African wolf. As a consequence, 44% of those interviewed suggested eliminating the African wolf as a solution to livestock losses, while 35.6% suggested more attentive guarding and 15.6% suggested reducing the number of sheep. Only 4.8% of respondents considered changing grazing land as a viable strategy to reduce stock losses.

Discussion

In the Guassa Mountains, Ethiopia, African wolves primarily fed on small rodent prey, plant material and insects, a diet similar to that reported for Eurasian golden jackals (Lanszki, Helati & Szabo, 2006; Jaeger *et al.*, 2007; Giannatos *et al.*, 2009). While carnivores primarily feed on meat, the high occurrence of plants is common in many carnivores including grey wolf, coyote (*Canis latrans*) and red fox (*Vulpes vulpes*) (Lanszki, Helati & Szabo, 2006; Stahler, Smith & Guernsey, 2006; Jaeger *et al.*, 2007). As livestock and domestic animals accounted for <5% of the diet, African wolves appear to feed predominantly on natural prey.

The high occurrence of rodents in the African wolf diet suggests potential for competition with the Ethiopian wolf because the Afroalpine Murinae community are also the main prey of the Ethiopian wolf (Sillero-Zubiri & Gottelli, 1995; Ashenafi et al., 2005). In the Bale Mountains, rodents accounted for 96% of the prey occurrence the Ethiopian wolf diet, with Tachyoryctes macrocephalus, Arvicanthis blicki and Lophuromys the main prey species (Sillero-Zubiri & Gottelli, 1995). As the range of the African wolf overlaps the much more restricted range of the endangered Ethiopian wolf, significant potential for competition exists between the two species. Competition between different carnivores has been reported to lead to declines or extinction of certain species (Boitani, 1992; Lever, 1994; Creel & Creel, 1996), and this represents a clear conservation concern. Ad hoc observations suggested the African wolf ate rodents from traditional rodent traps in the farmland, and so the extent to which it hunts, as opposed to scavenges rodents, is not clear. Nevertheless, further investigation into the foraging ecology of the Africa wolf and the nature of potential interference competition with the Ethiopian wolf is needed to better understand the potential effects on the conservation and survival of both species.

Despite its reliance on natural food items, the African wolf was reported to be the most serious livestock predator in the Guassa highlands. Sheep accounted for 90% of the reported livestock predated, mostly by African wolf, with the majority of predation events occurring in the dry season (November-February). The increased predation intensity at this time may be due to low natural abundance of rodents. High livestock predation rates at times of low natural prey abundance have been reported from several studies (Karani, 1994; Polisar et al., 2003; Woodroffe et al., 2005), and low rodent abundance in the dry season has been reported in the Bale Mountains during the dry season (Tallents, 2007). Furthermore, sheep in Guassa may get closer to bushland for grazing in the dry season as grass in the open Afroalpine meadows is scarce and dry, increasing their exposure to predators. Such seasonal effects on livestock predation due to ecological impact on grazing land are well reported (Coutinho & Campos, 1996; Van Bommel et al., 2007; Sandra, Cavalcant & Gese, 2010). Given that the period of high predation on livestock also coincides with the higher energetic demands of lactation (McNab, 1989) and increased food intake (Laurenson, 1995) due to the birth period of the African wolf, a series of factors may contribute to the higher risks to livestock during this period.

Mazzoli, Graipel & Dunstone (2002) reported that livestock predation by mammalian carnivores is the most important reason for the global decline of wild carnivores. In the Guassa Mountains, local people responded to livestock predation by killing the African wolf, particularly during their breeding season when they can be easily targeted with their puppies at den sites. With little law enforcement and protection for the African wolf, its population size in the Guassa mountains is likely to be controlled by the local community who eliminate pups whenever a den is located. Such lethal control has been widely reported as a response to depredation in a range of communities leading to severe population declines in many large carnivore species (Woodroffe & Ginsberg, 1998; Kruuk, 2002; Mitchell, Jaeger & Barrett, 2004; Woodroffe & Frank, 2005).

In subsistence livestock farming areas throughout much of Africa, improving livestock husbandry to reduce livestock depredation and helping local communities to develop positive attitudes towards large carnivores can have significant conservation outcomes (Ogada et al., 2003; Romanach, Lindsey & Woodroffe, 2007). In the Guassa highlands, the development of livestock grazing practices that minimize the contact between African wolf and sheep from February to April when 70% of livestock predation occurs could greatly reduce livestock losses and associated economic losses. In turn, this could improve attitudes towards these carnivores. Over 80% of households held negative attitudes towards the African wolf with over 40% suggesting eliminating the African wolf was the most appropriate response to depredation. In contrast, over 80% of respondents had positive attitudes towards the Ethiopian wolf despite identifying it as a livestock predator. Similar predation rates by Ethiopian wolves have also been reported in the Simien Mountains (Yihunie, 2006) without the species perceived as problem by the local community and attitudes towards wolves were in general positive (Ashenafi, 2001; Marino, 2003; Yihunie, 2006). The relatively lower predation rate by Ethiopian wolf and longstanding conservation actions across Ethiopia may have influenced the more positive attitudes of the local community towards this species. This suggests that improved perceptions are possible but that much work is needed to change the attitude of local communities towards the

African wolf. Tessema *et al.* (2007) proposed several conservation activities, including education campaigns, income-generating actions via ecotourism to generate employment opportunities and improving the involvement of local community in park management as possible options for improving attitudes to African wolves.

The relatively low livestock predation by spotted hyaenas in the Guassa Mountains is in contrast to the Bale Mountains where hyaena accounted for 57% of livestock kills reported and 84% of the economic loss (Atickem et al., 2010). The differences may emerge from the use of stonewalled enclosures (bomas) for livestock during the night in the Guassa Mountains. In the Bale Mountains, cattle were kept in the open near the household or in shabbily built wood enclosures with domestic dogs for protection (Atickem et al., 2010). While ineffective, this also remains the most important conservation threat for the survival of Ethiopian wolf, as domestic dogs of the herders act as vectors for rabies and canine distemper virus (Haydon et al., 2006; Randall et al., 2006). Improving husbandry methods, therefore, could provide significant benefits to all large carnivores in Ethiopia.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Education level of respondents.



CAPTURE AND IMMOBILIZATION OF AFRICAN WOLVES (CANIS LUPASTER) IN THE ETHIOPIAN HIGHLANDS

Authors: Gutema, Tariku Mekonnen, Atickem, Anagaw, Lemma, Alemayehu, Bekele, Afework, Sillero-Zubiri, Claudio, et. al.

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Capture and Immobilization of African Wolves (*Canis lupaster*) in the Ethiopian Highlands

Tariku Mekonnen Gutema,^{1,9,10} **Anagaw Atickem**,^{1,2} **Alemayehu Lemma**,³ **Afework Bekele**,⁴ **Claudio Sillero-Zubiri**,⁵ **Dietmar Zinner**,² **Wenche Kristin Farstad**,⁶ **Jon M. Arnemo**,^{7,8} **and Nils C. Stenseth**^{1,4} ¹Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, PO Box 1066, Blindern, NO-0316 Oslo, Norway; ²Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany; ³College of Veterinary Medicine and Agriculture, Addis Ababa University, Debre Zeit, PO Box 34, Debre Zeit, Ethiopia; ⁴Department of Zoological Sciences, Addis Ababa University, PO Box 1176, Addis Ababa, Ethiopia; ⁵Wildlife Conservation Research Unit, Zoology Department, University of Oxford, Recanati-Kaplan Centre, Tubney House, Tubney OX13 5QL, UK; ⁶Department of Production Animal Clinical Sciences, Faculty of Veterinary Medicine, Norwegian University of Life Sciences, PO Box 8146, NO-0033 Oslo, Norway; ⁷Department of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, Campus Evenstad, NO-2480 Koppang, Norway; ⁸Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83, Umeå, Sweden; ⁹Jimma University, College of Agriculture and Veterinary Medicine, Department of Natural Resources Management, PO Box 307, Jimma, Ethiopia; ¹⁰Corresponding author (email: jtarikumg@gmail.com)

ABSTRACT: We captured 14 individual African wolves (Canis lupaster) a total of 16 times in the Ethiopian Highlands in April 2015 and March 2016 by using rubber-lined foothold traps and immobilized them with dexmedetomidine-ketamine. Traps were baited with sheep meat and surveyed every 2 h. Capture efficiency (number of captures per number of visits) was 0.94, and capture rate (number of captures per number of trap nights) was 0.24. Trapped wolves were immobilized with 0.025 mg/kg dexmedetomidine and 8-10 mg/kg ketamine on the basis of respective estimated body mass. Mean (SD) induction times were 3.4 (0.5) min for subadults (n=4), 3.5 (0.3) min for adult males (n=4), and 4.7 (1.0) min for adult females (n=6). Inductions were calm, muscle relaxation was good, and all animals were completely immobilized. Apart from increased rectal temperatures, no major negative side effects were observed. Atipamezole at 10 mg intramuscularly per milligram of dexmedetomidine administered was used for reversal at a mean of 43.5 (7.7) min after administration of dexmedetomidine-ketamine. Recoveries were relatively smooth, and animals were on feet, leaving the site within a mean of 13.6 (3.9) min, after atipamezole administration. Our results indicate that African wolves can be safely captured and immobilized by using rubber-lined foothold traps and dexmedetomidine and ketamine.

Key words: Canis lupaster, dexmedetomidine, Ethiopian wolf, foothold traps, immobilization, ketamine.

Free-ranging canids are captured for research and management purposes. Typically, animals are trapped before administration of anesthetic drugs to enable safe handling (Larsen and Kreeger 2014). Physical restraint and induction of anesthesia are stressful procedures and require the use of optimal methods, equipment, and drugs (Caulkett and Arnemo 2015). Different physical capture techniques have been used in canids, depending on the target species, habitat, and available resources and expertise. For instance, foothold traps proved to be effective in capturing side-striped jackals (*Lupulella adusta*), blackbacked jackals (*Lupulella mesomelas*), and Ethiopian wolves (*Canis simensis*; Sillero-Zubiri 1996).

A combination of medetomidine and ketamine has been widely used to immobilize free-ranging canids (Kreeger and Arnemo 2012). Medetomidine is a potent alpha-2 adrenoceptor agonist that produces sedation, analgesia, and muscle relaxation. Combined with a relatively low dose of ketamine, it induces anesthesia (Larsen and Kreeger 2014). Medetomidine is composed of equal parts of two optical enantiomers (dexmedetomidine and levomedetomidine), but its pharmacologic effects are due almost exclusively to dexmedetomidine (Ansah et al. 1999). Although dexmedetomidine may have clinical benefits compared with medetomidine as a sedative in dogs (Kuusela et al. 2001), recent studies on dexmedetomidine and medetomidine as adjuncts to anesthesia in brown bears (Ursus arctos) are contradictory (Fandos Esteruelas et al. 2017). A new wolf species, the African wolf (Canis lupaster), was discovered in the Ethiopian Highlands in 2011 and



FIGURE 1. Map showing the study areas in the Ethiopian Highlands where African wolves (*Canis lupaster*) were captured in April 2015 and March 2016 by soft leghold trapping and immobilized with dexmedetomidine and ketamine. masl=meters above sea level.

confirmed as a distinctive species that diverged over a million years ago from its ancestral canids (Koepfli et al. 2015). Here, we report the safe capture and immobilization of free-ranging African wolves by using rubber-lined foothold traps and dexmedetomidine-ketamine.

We trapped African wolves in the Guassa Community Conservation Area $(10^{\circ}27'\text{N}, 39^{\circ}45'-39^{\circ}49'\text{E})$ in April 2015 at three sites approximately 1.4 km from each other and in the Borena Saynt National Park $(10^{\circ}50'-10^{\circ}53'\text{N}, 38^{\circ}40'-38^{\circ}54'\text{E};$ Fig. 1) in March 2016 at three sites approximately 2.5 km from each other. The Guassa Community Conservation Area has an area of 111 km² with an elevation of 3,200–3,700 m. The Borena Saynt National Park comprises 132 km² at an elevation of 1,900–3,700 m. Both areas are habitats for the world's rarest canid, the Ethiopian wolf, which is endemic to the Ethiopian Highlands.

We used rubber-lined Soft Catch foothold traps (Woodstream Corporation, Lititz, Pennsylvania, USA) sizes 1.5 and 3. The traps were set in the buffer zone of the respective protected areas. African wolves were frequently observed in these areas, whereas

Ethiopian wolves were rarely seen during our 3 mo of assessment of the distribution of canids. Two foothold traps were buried on a 1-m² plot free from stones and other potentially harmful materials. Each trap was anchored with two metal sticks buried about 60 cm into the ground. The traps were set from 1600 hours to 0600 hours and checked every 2 h to reduce risk of stress and injuries in trapped animals and to release nontarget species, in particular the Ethiopian wolf. During each trapping session, four to eight trap stations were set up with sheep meat as bait (Rowe-Rowe and Green 1981; Kaunda 2001). Once trapped, the wolves were covered by a blanket and manually restrained for administration of 0.025 mg/kg of dexmedetomidine (Dexdomitor[®] 0.5 mg/mL, Orion Pharma Animal Health, Turku, Finland) followed by 8 mg/kg of ketamine (subadults) or 10 mg/kg of ketamine (adults; Ketamine® 50 mg/mL, Rotexmedica, Trittau, Germany) on the basis of estimated body weights. The drugs were injected into the semimembranosus muscle by using a handheld syringe. The induction time (time from administration of dexmedetomidine-ketamine to no response to handling) was recorded. To evaluate capture

			Adults	Subadults		
Variable	Units	Males $(n=6)$	Females (n=4)	Range	<i>n</i> =4	Range
Body mass	kg	9.0 (0.6)	8.1 (0.7)	7–10	6.8 (0.54)	6-8
Dexmedetomidine	mg/kg	0.026	0.029	0.02-0.03	0.030	0.029-0.03
Ketamine	mg/kg	8.35(0.47)	8.36 (0.53)	8–9	8.81(1.35)	8-10
Induction time	min	3.5(0.3)	4.7(1)	3-6	3.4(0.5)	3–4
Respiratory rate	beats/min	17(1)	18(3)	14-20	16 (3)	12-18
Heart rate	beats/min	78(9)	86 (7)	70–96	89 (25)	70-126
Body temperature	С	41.0 (1.3)	40.1(1.7)	37-41	39.1 (0.8)	38-40
Time to reversal	min	51.0 (11.1)	53.5 (4.7)	43-67	46.0 (5.4)	40-53
Ear movements	min	6.0(0.4)	6.7(2.7)	5-11	6.0(1.7)	4-9
On feet (start leaving)	min	15.5 (4.9)	14.2 (3.6)	10-22	10.7 (2.5)	8–13

TABLE 1. Summary statistics for African wolves (*Canis lupaster*) immobilized with dexmedetomidine-ketamine in the Ethiopian Highlands in April 2015 and March 2016.^a

^a Atipamezole at 10 mg per milligram of dexmedetomidine was given for reversal. Values are presented as means (SD) and ranges.

efficiency of the traps, the number of captured animals per visit was calculated (Kamler et al. 2008). In addition, we calculated capture rate as the number of captures divided by the number of trap nights (number of traps multiplied by number of nights; Rowe-Rowe and Green 1981; Kaunda 2001).

Immobilized wolves were wrapped in a blanket to maintain body heat, as recommended by Sillero-Zubiri (1996). The ambient temperature during the capture ranged from 1 C to 8 C. Animals were weighed, and their reproductive condition was assessed. Heart rates (using a stethoscope), respiratory rates (counting chest movements), and rectal temperatures (using a digital thermometer) were recorded once the animal became immobilized and failed to respond to stimuli. All animals were examined by an experienced veterinarian for possible trauma, especially to teeth and feet. Animals were classified as adults or subadults based on tooth wear (Landon et al. 1998). All wolves were fitted with a very high frequency radio collar (Telemetry Solutions, Concord, California, USA).

For reversal of immobilization, we administered 10 mg of atipamezole per milligram of dexmedetomidine (Antisedan[®] 5 mg/mL, Orion Pharma Animal Health) intramuscularly in the thigh, and we recorded the time to reversal (time from administration of dexmedetomidine-ketamine to injection of atipamezole). Recoveries were observed, and the times from administration of atipamezole to first signs of arousal (ear movements), and standing and starting to leave the site (on feet and leaving) were recorded.

Fourteen wolves were trapped, 10 adults (three males and seven females) and four subadults (two males and two females). Two of the females were trapped twice. Also, two domestic dogs were captured. On average, six traps were set at each site for 11 d. During 66 trap nights, 16 wolves were captured. The capture efficiency was 94%, and capture rate was 24%. Most of the wolves (94%) were captured between 1700 hours and 2300 hours, whereas 6% were captured between 0400 hours and 0600 hours. Summary statistics for body mass, physiologic variables, drug doses and effects, and recovery were collected (Table 1). Inductions were calm, and muscle relaxation was good. Most immobilized animals had higher rectal temperatures than expected, and some were considered hyperthermic (rectal temperature above 40 C). The blanket was, therefore, removed. No other obvious side effects were observed. None of the wolves needed additional drugs to maintain immobilization. No trauma from the traps was observed. Recoveries were relatively smooth, and all wolves left the capture site 10-22 min after atipamezole administration. All wolves survived for at least 1 yr. Hence, the rubber-lined Soft Catch foothold traps used in this study appeared to be an effective and safe method for the capture of African wolves. Our results supported the importance of this method, which has been used for a wide range of carnivore species, including Ethiopian wolves (Sillero-Zubiri 1996). We captured no Ethiopian wolves, regardless of their presence in close vicinity of the trapping site. In human-dominated landscapes, carnivore activity is influenced by human activities, and a certain period of the day might provide the highest capture rates (Virgós et al. 2016). In our study, the highest capture rate was recorded between 1700 hours to 2300 hours, which is a suitable period for trapping African wolves in the Ethiopian Highlands.

A combination of dexmedetomidine and ketamine was effective for immobilization of African wolves. Inductions were fast, duration of immobilization was sufficiently long for all procedures to be completed, and recoveries were relatively quick and smooth after administration of atipamezole. The main side effect was hyperthermia. Rectal temperatures higher than 40 C are cause for concern, and attempts should be made to cool the animal (Caulkett and Arnemo 2015). In future studies on African wolves, the rectal temperature should be measured in 5- to 10-min interval to detect thermoregulatory problems. Also, monitoring for respiratory depression (e.g., with pulse oximetry) is recommended. Supplemental oxygen should be available in case of hypoxemia. Admasu et al. (2004) used a relatively high dose of medetomidine (0.09 mg/kg, equivalent to 0.045 mg/kg of dexmedetomidine) and a low dose of ketamine (2.8 mg/kg) to anesthetize seven African wolves. Inductions (5.0 min) were longer than in our study. Recoveries, however, were quicker, and the wolves moved away 6.3 min after reversal with atipamezole (0.45 mg/kg), most likely due to the low dose of ketamine. Adamsu et al. (2004) found no obvious adverse effects of anesthesia but did not report data on physiologic variables. Medetomidine (0.09 mg/kg)

and ketamine (1.5 mg/kg) were also used to immobilize Ethiopian wolves for vaccination (n=77) and revaccination (n=19) against rabies (Knobel et al. 2008), but the authors gave no details on anesthetic effects or recoveries after reversal with atipamezole. On the basis of the 1–2 yr follow-up (radio tracking, observations, and behavior) of our animals, there were no apparent long-term effects from the captures. In conclusion, we recommend rubber-lined Soft Catch foothold traps and dexmedetomidine-ketamine and atipamezole for capture and reversible immobilization of African wolves.

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