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Densities of spotted hyaena (*Crocuta crocuta*) and African golden wolf (*Canis anthus*) increase with increasing anthropogenic influence

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Abstract

We report densities of spotted hyaena (*Crocuta crocuta*) and African golden wolf (*Canis anthus*) in Enderta district in northern Ethiopia with high human and low natural prey densities. We estimated spotted hyaena and African golden wolf abundance and characterized their spatial distribution with three methods: we surveyed four road-transects for 66 nights during dry (n=41) and wet (n=25) seasons, we used 34 calling stations and we mapped all active spotted hyaena dens at the time of the survey. The density of spotted hyaena and African golden wolf increased with proximity to towns where human density was higher. A total of 562 spotted hyaena and 63 African golden wolf responded to calling stations, leading to estimates of 1,145 spotted hyaena and 166 African golden wolf in Enderta district. This method also found a significantly higher spotted hyaena and African golden wolf abundance in high human density areas. Maximum response radius was 2.8 km for spotted hyaena and 2.5 km for African golden wolf, and response probability was 0.83 for spotted hyaena and 0.8 for African golden wolf, respectively. We found 40 active spotted hyaena dens with 1,507 remnants of prey, and the majority of the dens were located close to rivers and villages. Our findings show a positive relationship between spotted hyaena, African golden wolf and human concentrations that might demonstrate a case of exceptional coexistence of humans and carnivores, both at high densities. We suggest further investigations into co-adaptations between humans and predators in the study area.

Key-words: abundance, carnivores, density, human-carnivore coexistence, human-carnivore conflict, prey depleted landscapes

Introduction

In protected areas, carnivore density is strongly related to the available natural prey biomass (Karanth et al. 2004; Khorozyan et al. 2008) while in human-dominated landscapes carnivore density depends on the available anthropogenic resources (Gehrt et al. 2010; Luis Llanez 2012; Yirga et al. 2013). When these anthropogenic food resources are abundant and human persecution is low, large carnivores can reach densities even greater than their densities in the wild (Athreya 2012). Occurrence and persistence of carnivores like spotted hyaena (*Crocuta crocuta,*) and golden jackal (*Canis aureus* and *Canis anthus*) in anthropogenic landscapes is associated with availability of anthropogenic food sources (Woodroffe and Ginsberg 1998; Fuller and Sievert 2001; Basille et al. 2009). Predators including spotted hyaena and golden jackal are able to persist at high human densities and at high levels of landscape transformation (Linnell et al. 2001; Cardillo et al. 2004; Blanco and Corte´s 2007; Basille et al. 2009; Agarwal et al. 2010).

Spotted hyaenas show high behavioral and ecological plasticity that help them to live in close proximity to humans (Woodroffe 2000; Sunquist and Sunquist 2001; Boydston et al. 2003). They inhabit very wide historical ranges with relatively stable populations across Africa (Kolowski and Holekamp 2009) and are opportunistic carnivores that feed on locally abundant prey species (Cooper et al. 1999). Spotted hyaenas live in societies that are large (up to 90 hyenas in a clan) and more complex than any other carnivores (Kruuk 1972; Holekamp et al. 2007). The mean clan size across Africa is approximately 21 hyaenas (Smith and Holekamp 2010). Sizes of subgroups of spotted hyaenas range from one to tens of animals (Holekamp et al. 2000). These subgroups are important for cooperative activities as territorial defense (Tilson and Hamilton 1984; Frank 1986; Henschel and Skinner 1991; Boydston et al. 2001). Spotted hyaenas often congregate at a communal den (Boydston et al. 2003). Dens serve important protective functions such as the sheltering of cubs, which usually spend their first 8–12 months of life at dens (Holekamp and Smale 1998). Dens also have important social functions. For instance, cubs form relationships with both peers and adults at dens, and dens serve as meeting points for adults (Holekamp et al. 2000). However, it is poorly known how spotted hyaenas select den sites in human-dominated landscapes.

The golden jackal (*Canis anthus and Canis aureus*) is found in many areas of Africa, Europe and Asia (Sillero-Zubiri et al. 2004) and is able to live in human-dominated agricultural landscapes (Šálek et al. 2014). Due to their habitat plasticity and opportunistic feeding habits, golden jackals inhabit a variety of different habitat types (Stoyanov 2012; Giannatos 2004; Jhala and Moehlman 2004). Golden jackals venture into human habitations at night to feed on human organic waste (Jhala 2008). They are common throughout their range and high densities are observed in areas with abundant food and cover (Jhala 2008). Despite its widespread distribution, there is very little quantitative information on golden jackal abundance, habitat use, and ranging patterns in relation to food availability (Sillero-Zubiri et al. 2004; Jhala 2008).

The African golden wolf (*Canis anthus*) and Eurasian golden jackal (*Canis aureus*), were originally thought to be the same species, formerly known as the golden jackal (Koepfli et al. 2015). African and Eurasian golden jackals are genetically distinct lineages and African golden jackals merit recognition as a distinct species (Koepfli et al. 2015). Two recent studies reported that the larger-sized golden jackals from Ethiopia and North and West Africa were more closely related to gray wolves than to other populations of golden jackals (Rueness et al., 2011; Gaubert et al., 2012). The small, golden-like jackal from eastern African is actually a small variety of a new species, distinct from the gray wolf, that has a distribution across North and East Africa, and this previously unrecognized species is named the African golden wolf **(***Canis anthus***)** (Koepfli et al. 2015). According to this report taxonomists had mistaken African and Eurasian golden jackals for the same species because of a high degree of similarity in their skull and tooth morphology. According to Koepfli et al. (2015), the golden-like jackal from Enderta district, northern Ethiopia is most probably the African golden wolf **(***Canis anthus***)** hereafter called golden wolf.

Spotted hyaena and the golden wolf are common carnivores across Enderta district, and can easily be seen almost every night at the outskirts of the city. We sought to establish spotted hyaena, golden wolf and human abundance relationships and map spotted hyaena dens in human-dominated landscapes. We also investigated spotted hyaena and golden wolf spatial distribution patterns.

Study area

The study was conducted within Enderta district of Tigray region, northern Ethiopia (Fig 1). The district is located between 13^0-14^0 North and at 39^0-40^0 30′ East; it has a population density of 79 persons km^{-2} and an average family size of five (Sara 2010). Altitude ranges from 1,400 to 2,700 m.a.s.l. and the landscape is mountainous, with undulating, flat and plain lands, rugged valleys and gorges, and hilly areas (Sara 2010). The district has a total surface area of 1,416 km^2, of which permanent rainfed agriculture covers 49 %; the remaining area is too arid or too steep for agriculture and most of it is used for grazing. The average land holding size per household is

0.75 hectare and more than 80 % of the population is engaged in subsistence farming (Sara 2010). Due to chronic food insecurity, many of the households are at least partly dependent on food-aid. Rainfall of the area is bimodal: a short rainy season between January and April, and a long rainy season from June to August with an average annual rainfall of 550 mm. The mean maximum temperature ranges between 12 and 27^{o} C. In the northern highlands of Ethiopia, forests have been completely converted into farms and grazing lands over the last few centuries except for patchy remnants of old aged Afromontane forests around most Ethiopian Orthodox Tewahido Churches (Aerts et al. 2007; Alemayehu 2007). These fragmented church forests are widely distributed habitat patches, and spotted hyaenas hide in these church forests during the day. The church forests have traditionally and religiously been protected for centuries.

Methods

Road Transect survey

We monitored four road transects every month from March to August, 2012 to record spotted hyaena and golden wolf sightings. Transects centered around the city of Mekelle (regional capital) and started at the outskirts of town (urban center). The first (23 km) went East to Adikolo; the second (38 km) went South to Adigudom; the third (36 km) went North to Wukro; and the last (19 km) went East from Quiha (Mekele agglomeration) to Aragure. We started the transect survey at dusk and usually ended around 2100-2200h (GMT+3). We noted during the survey all encountered spotted hyaenas and golden wolves as well as moon phase, season, start and finish time, time of the sighting, distance from viewer (estimate by observers) to the animal and the distance from the beginning point of the driving. We surveyed transects during dry (March through May) and wet (June through August) seasons in a vehicle at a speed of 30 km per hour. Two team members standing at the back of the vehicle with powerful torches (Maglite

LED) were scanning right and left sides (covering approximately 600 m width of transect) for spotted hyaena and golden wolves; in case of doubt a team member would run towards these animals carrying a torch to confirm species. The research team had torches, GPS (Garmin E-trex) and night vision Binoculars (Yukon Ranger 5x42 LT). We placed transects along the main roads because other areas were not accessible and were difficult to drive.

Abundance and distribution survey

We surveyed spotted hyaena and golden wolf abundance and distribution using 34 randomly selected calling stations from 25 March to 4 April in 2012. A calling station survey is an effective and inexpensive technique for counting spotted hyaena and lion (Ogutu and Dublin 1998; Mills et al. 2001; Maddox 2003; Bauer 2007) and jackal (Ogutu 1994; Maddox 2003) in African ecosystems. We played continuous gnu- hyaena distress calls and spotted hyaena sounds for an hour on an MP3 player connected to a megaphone (Monacor 45) placed on the roof of a vehicle. We performed two cycles of 20 minutes broadcast followed by ten minutes pause and rotated the speaker 90° after 5 minutes broadcast to provide 360° coverage. For optimal visibility, we placed calling stations in open areas. Four observers counted responding spotted hyaena and golden wolf using torches immediately after the last broadcast. We placed calling stations at least 7 km apart to ensure that the same individual was not called in at multiple sites.

Estimation of predator abundance and density

The total population size of spotted hyaena and golden wolf was estimated using the model of Mills et al. (2001) and Ogutu et al. (2005). The expected number of spotted hyaena and golden wolf within the response range (u) was estimated by

$$u_s = y_s / S_s \tag{1}$$

Where y is the mean number of carnivores for species s responding per station and S is the response probability of each species from the calibration experiments (Mills et al. 2001; Ogutu et al. 2005). The total number of spotted hyaena (NT) and golden wolf in Enderta district was estimated using the relation

$$NT = (AH/AS)\ u \qquad (2)$$

Where AH =the area of the entire district and AS =the area sampled around a call-in station (Mills et al. 2001; Ogutu et al. 2005).

Calibration experiments

We estimated call-up maximum response range and probability for spotted hyaena and golden wolf following Mills et al. (2001) and Ogutu et al. (2005) through calibration experiments. We performed independent call-ups to estimate the distance from which spotted hyaena and golden wolf were attracted to broadcasts in the following habitats: area exclosure (partially protected areas of a few hectares dotted across the landscape), open agricultural area, human settlement and garbage dumping area. We conducted calibration experiments for spotted hyaenas and golden wolf to estimate maximum response range and response probability (% of spotted hyaenas and golden wolves responding within range) after the abundance and distribution survey. Calibration experiments were conducted in non-survey areas (places where broadcasts had not been done during the abundance and distribution survey).

To minimize the likelihood of habituation (Ogutu and Dublin 1998; Mills et al 2001; Maddox 2003), we looked for spotted hyaenas and golden wolves in non-survey areas. One vehicle stayed with the animals to record their reaction while the other drove away and conducted the broadcast as done during the call-in surveys. We played the tape at 4.0, 3.5, 3, 2.8, 2.6, 2.5, 2.3, and 2 km, with the megaphone facing in the direction of the target species. These tests were conducted by six observers in mobile communication.

Spotted hyaena den mapping

We located spotted hyaena dens that were active at the time of the survey across the district with the help of villagers, extension workers and wildlife experts; we probably mapped all dens in the study area since it is unlikely that any den would go undetected or unreported by people, even away from villages. We recorded habitat type, vegetation cover, grazing intensity, distance to the nearest watercourse/river, village and urban center, den condition (active or abandoned; determined by the presence of fresh scats, fresh food remnants and fresh traces), human disturbance, protection circumstance as well as livestock damage in and around the spotted hyaena dens. We examined fragments of bone, tooth, hoof, horn and skin found within the dens and outside within a 10 m radius and identified them in situ whenever possible (implying surface collection of all visible remains). We recorded GPS coordinates of the exact locations of all spotted hyaena dens.

We used the JMP 5 software package (SAS Institute, Cary, NC) for statistical analyses. Nonparametric Wilcoxon tests were used to compare spotted hyaena and golden wolf encounters along road transects during the wet and dry seasons. We correlated spotted hyaena and golden wolf encounters and distance traveled along road transects from high human density areas.

Results

Relationship between carnivore and human abundance

We encountered 871 spotted hyaenas (441 dry season, 430 wet season) and 307 golden wolves (215 dry season, 92 wet season) in 66 survey nights (41 dry season, 25 wet season) along four road transects. The number of observations was significantly higher in the dry season for golden wolf ($p<0.001$) compared to the wet season (Table 1). The numbers of observations for spotted hyaena in the dry and wet seasons were similar ($p>0.05$) (Table 1). The mean distances from the viewer to spotted hyaena and golden wolf were approximately 88 and 45 m (dry season) and 69 and 38 m (wet season), respectively. Densities of spotted hyaena and golden wolf increased with increasing anthropogenic influence (presence of organic waste and livestock) in all roads transect. The number of spotted hyaena and golden wolf encountered was higher with proximity to towns where human density was higher (Fig 2, 3). Wukro, Agula, Adigudom, and Meremieti were towns with very high human density in the section of transect (Fig 2).

Response range and response probability

We conducted 18 calibration experiments for spotted hyaenas and one calibration experiment for golden wolves and found a total of 102 spotted hyaenas and 15 golden wolves. We used one independent calibration experiment to estimate golden wolf response range and probability where 12 out of 15 golden wolves responded at a radius of 2.5 km. No response from golden wolves was observed beyond that. It was quite difficult to get more independent experiments for golden wolves due to the mobility of the animal. Maximum response radius was 2.8 km for spotted hyaenas (Table 2). Thus, each calling station covered an area of 24.62 km^2 for spotted hyaena and 19.63 km^2 for golden wolf. Response probabilities were 0.83 ± 0.17 (mean ± SD) for spotted hyaena (n=15) and 0.8 for golden wolf (n=1), respectively (Table 2). The majority (67 %) of the calibration experiments were conducted in open agricultural areas. We assumed that both the response range and the response probability were the same in all habitats irrespective of the landscape of the district.

Abundance and density of predators

A total of 562 spotted hyaena and 63 golden wolf responded to the calling stations; the majority of spotted hyaena (55 %, n=309) were found in human settlements and waste dumping areas while the majority of golden jackals (67 % n=42) were found in human dominated open agricultural areas (Table 3). Abundance of spotted hyaenas and golden wolves increased with increasing anthropogenic influence (presence of human organic waste and livestock). The mean number of spotted hyaenas and golden wolves responding per calling station were 19 (range 0-150) and 3 (0-7), respectively. Spotted hyaena and golden wolf were seen at 30 (88 %) and 24 (70.6 %) of the calling stations during the survey, respectively. The highest number of spotted hyaenas (150) was in a garbage dumping site; this was the only calling station where it was difficult to accurately count them and 150 is a conservative estimate.

Approximately 837 km^2 (59 %) and 667 (47 %) km^2 were covered by 34 calling stations for estimating spotted hyaena and golden wolf, respectively. Therefore, assuming a uniform response range and probability across the district, the overall spotted hyaena density was 0.8 spotted hyaena/km^2 for a total of 1,145 spotted hyaena (17 ± 26) (mean ± SD). Golden wolf density over the entire district was estimated as 0.12 golden wolf /km^2 or a total population estimate of 166 golden wolf (1.6 ± 1.8) (mean ± SD). Spotted hyaena density was 74 times higher in the garbage dumping site than in natural areas. Similarly, golden wolf density was highest in the garbage dumping site and lowest in the natural bushy area (Table 3).

Spotted hyena den mapping

A total of 40 active spotted hyaena dens at the time of the survey were assessed and most (85 %) were located approximately 1 to 2 km from a nearby village (Table 4). They were primarily located in close proximity to high human density areas (1.49 km ± 0.94) and the nearest water source (1.15 km ± 1.48) (mean ± SD). Each den had more than one entrance and almost all the cave and burrow den types had sections. Vegetation cover for most (72.5 %) of the dens was relatively very high and most dens were located (62.5 %) less than 1 km from the nearest stream (Table 4).

A total of 1507 (96 % unidentified) pieces of prey remains were found, and the rate of accumulation varied based upon the type of den (Fig 4, 5). The prey remains accumulated in caves and church forest were highest (Fig 5). Very few dens were found to contain large concentrations of bone: we found 24 cattle skulls, 10 donkey skulls, 534 bone fragments and 50 tooth fragments at a church forest located approximately 3 km from the waste dumping place of Mekelle city. Prey remnant counts ranged from 0 to 584. The church forest dens (n=6) had the highest bone fragment accumulation, with an average of 95.7 bone fragments. The cave dens (n=4) had an average of 93.8 bone fragments each, the burrow dens (n=2) had an average of 90 bone fragments each, and the area exclosure dens (n=6) had an average of 34.4 bone fragments each. The bush dens (n=4) had the lowest bone fragment accumulation, with an average of 7.3 bone fragments each. Most (91.7 %) of the fragments identified were livestock remains that included 27 skulls, five horns, three hooves of cattle and ten skulls of donkeys. Four teeth and two jaws of camels, and four hooves of sheep, goat and donkey were identified.

Discussion

Relationship between carnivores and human inhabitants

Our results of road transect monitoring, calling station survey and den mapping demonstrate a positive relationship between human and spotted hyaena density in prey depleted human-dominated landscapes. Spotted hyaena dens were located in close proximity to high human density areas. This relationship is likely driven by food resources such as livestock and waste. In contrast to Woodroffe (2000) who found a negative relationship between carnivore survival and human population density, we found a positive relationship between spotted hyaena, golden wolf and human concentrations in areas accompanied by high levels of human activity. The spatial dispersion of human settlements and their density across the landscapes might influence the density and occurrence of spotted hyaena and golden wolf. This suggests a unique preference of spotted hyaena and golden wolf to very high human density areas over areas with lower human density. There are two possible explanations: first, the local communities have a positive attitude towards spotted hyaena because spotted hyaenas are important in sanitizing the environment by foraging on household waste and removing potentially infected organic waste from human settlements (Abay et al. 2011; Yirga et al. 2015a.b) and as a consequence spotted hyaenas are more abundant in areas where human density is relatively high. Second, spotted hyaena survival in the area is almost entirely dependent on anthropogenic food around human concentrations (Yirga et al. 2012) because the natural prey base of the area is highly depleted. This unique coexistence of spotted hyaena and people is not found elsewhere in Africa and has not been reported for other large predators. Our findings support the conclusion that spotted hyena in Tigray region depend exclusively on anthropogenic resources and prefer anthropogenic over natural landscapes (Abay et al. 2011; Yirga et al. 2014). Our findings are in stark contrast to various studies indicating that carnivores including spotted hyaena avoid areas of elevated human activity mainly due to persecution and retaliation (Treves and Karanth 2003; Colyn et al. 2004; Reed and Merenlender 2008; Baker et al. 2008; Van Meter et al. 2009; Packer et al. 2009; Croes et al. 2011; Burton et al. 2011).

Response range, response probability and abundance

The sample size for estimating response probability and range for golden wolf is quite low (one calibration experiment) and is due to the mobility of the animals. Golden wolves were highly mobile in the landscape and this creates a problem for a vehicle to stay with the animals to record their reaction during the calibration experiment. However, we feel that the estimated response range and response probability of golden wolves is appropriate because the number of golden wolves we encountered during the calibration experiment was high enough to estimate response range and probability.

Response probability and range for spotted hyaena and golden wolf in human-dominated landscapes has not previously been reported. There are no estimates of response probability for predators in human-dominated areas and no comparisons of responses in protected and unprotected populations (Ogutu et al. 2005). Few attempts have been made to calibrate calling stations despite wide utilization to establish abundance, density and distribution of carnivores (Kruuk 1972; Mills 1985; Sillero-Zubiri and Gottelli 1992; Creel and Creel 1996; Mills and Gorman 1997; Ogutu and Dublin 1998).

The estimated maximum response range of 2.8 km for spotted hyaena in the human-dominated landscape was somewhat shorter than either the 3.2 km obtained by Mills et al. (2001) for Kruger spotted hyaenas, 3.7 km estimated by Creel and Creel (1996) for spotted hyaenas in Selous Game Reserve or 4 km estimated by Ogutu et al. (2005) for spotted hyaenas in the Mara ecosystem of Kenya, but similar to the 3 km estimated by Maddox (2003) for Kruger spotted hyaenas. A number of factors can affect response range such as topography, vegetation cover, battery used, volume of mp3 and megaphone, and human density.

The estimated response rate of 0.83 for spotted hyaena in the Enderta district was somewhat similar to the 0.88 estimated by Maddox (2003) in the Serengeti and 1.0 estimated by Creel and Creel (1996) in Selous Game Reserve in Tanzania. The probability of responding to calling stations might be inversely related to response range (Ogutu et al. 2005). The response probability of spotted hyaena in the Mara ecosystem of Kenya was estimated to be 0.583 by Ogutu et al. (2005), similar to the estimate of 0.61 by Mills et al. (2001). Response probabilities were similar in protected and in unprotected areas with human land uses (Ogutu et al. 2005). However, Boydston et al. (2003) noted that predator behavior can be affected by the presence of people.

Spotted hyaena and golden wolf abundance and density varied considerably among different locations of calling stations in the study area. Human settlements and garbage dumping areas supported a relatively high density of spotted hyaena among others perhaps due to availability of scavengeable food. The high number of spotted hyaenas at the garbage dumping areas suggests that spotted hyaenas may occupy different group territories around different den sites but then commute across other territories to a source of super-rich food. Spotted hyaenas are frequent visitors to garbage dumps and other sources of scavengeable food (Horwitz and Smith 1988; Leakey et al. 1999).

Spotted hyaena den selection

In the current study bush dens had the lowest bone fragment accumulation suggesting that spotted hyaena bone accumulation around bush dens is much more limited than around cave and church forest den locations. In this study 1507 pieces of prey remains predominantly occurred in caves and church forests. This is perhaps due to the permanence of the areas; the longer the time span of the den the more bones will accumulate (Pokines and Peterhans 2007). Surface bone concentration around a spotted hyaena cave den located in Amboseli National Park, Kenya, reached up to 75 bone pieces per m^2; from 2,017 specimens, 56 individuals were identified (Hill 1983, 1989). Surface bone concentration around burrow dens is less compared to around caves.

Caves shelter adult spotted hyaenas and encourage bone accumulation while burrow dens are often more difficult to enter and are used to deposit juveniles (Pokines and Peterhans 2007).

Spotted hyaenas in our study area transport carcass portions into church forests. We found 24 skulls of cattle and ten skulls of donkey in a church forest that was approximately 3 km from the garbage dumping area of Mekelle. It is more likely that these skulls of livestock are collected from the garbage dumping area where spotted hyaenas are known to scavenge every night. This indicates that spotted hyaenas transport bones into dens, perhaps for their offspring. Juvenile spotted hyaenas are vulnerable and do not leave the den until 9–12 months old (Lansing et al. 2009). Other studies have shown significant accumulation of bones at spotted hyaenas dens (Bunn 1983; Hill 1989; Boydston et al. 2006). Human remains in a spotted hyaenas cave den located approximately 3.2 km from a hospital cemetery were found in Kajiado, Kenya (Sutcliffe 1969, 1970). This shows that spotted hyenas can also accumulate human remains from a nearby cemetery; there were no reports of spotted hyaenas killing people.

In this study a few dens were found to contain large concentrations of bone, and most of these dens were located within 1 to 3 km from the garbage dumping area of Mekelle. This suggests that the bones accumulated were collected from waste dumps, not obtained from predation. Dens were predominantly located along water resources and villages. Other studies also found that spotted hyaena dens were located close to permanent water resources (Mills 1990; Boydston et al. 2003; Boydston et al. 2006). The location of water sources is suggested to influence movements of spotted hyaenas in arid areas (Tilson and Henschel 1986; Cooper 1989). In the dry season, spotted hyaenas in the Serengeti National Park, Tanzania selected dens located in the direction of large prey herds (Kruuk 1972). These confirm that spotted hyaenas are restricted by water and food distribution. In our study spotted hyaena dens were located with significant proximity to human settlements where spotted hyaenas have access to human waste and livestock.

Conclusion

Our assessment of road transects, calling station surveys and den mapping have shown spotted hyaena-human relationship and distribution patterns along human-dominated areas. Our results demonstrate the value of road transect monitoring which provides reliable information to establish relationships between spotted hyaena, golden wolf and human concentrations in anthropogenic landscapes. Road transect surveys are relatively expensive and time consuming. Calling stations have the potential to offer much more reliable information on spotted hyaena and golden wolf abundance and density comparatively at low costs and short time, and would also be important to assess distribution patterns. Den mapping provides insights about den selection and location. It is through these more intensive studies that we establish the relationship between spotted hyaena, golden wolf and human inhabitants in anthropogenic landscapes. We conclude that there is a positive relationship between spotted hyaena, golden wolf and human abundance and density in prey depleted anthropogenic landscapes in northern Ethiopia. Our findings show that spotted hyaena persist at very large densities with great affinity for high human density locations, a case of exceptional coexistence of humans and carnivores, both at large densities.

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Ethical statement

- The manuscript has not been submitted to more than one journal for simultaneous consideration.
- The manuscript has not been published previously (partly or in full).
- A single study is not split up into several parts to increase the quantity of submissions and submitted to various journals or to one journal over time (e.g. "salami-publishing").
- No data have been fabricated or manipulated
- No data, text, or theories by others are presented as if they were the author's own ("plagiarism").
- Proper acknowledgements to other works are given.

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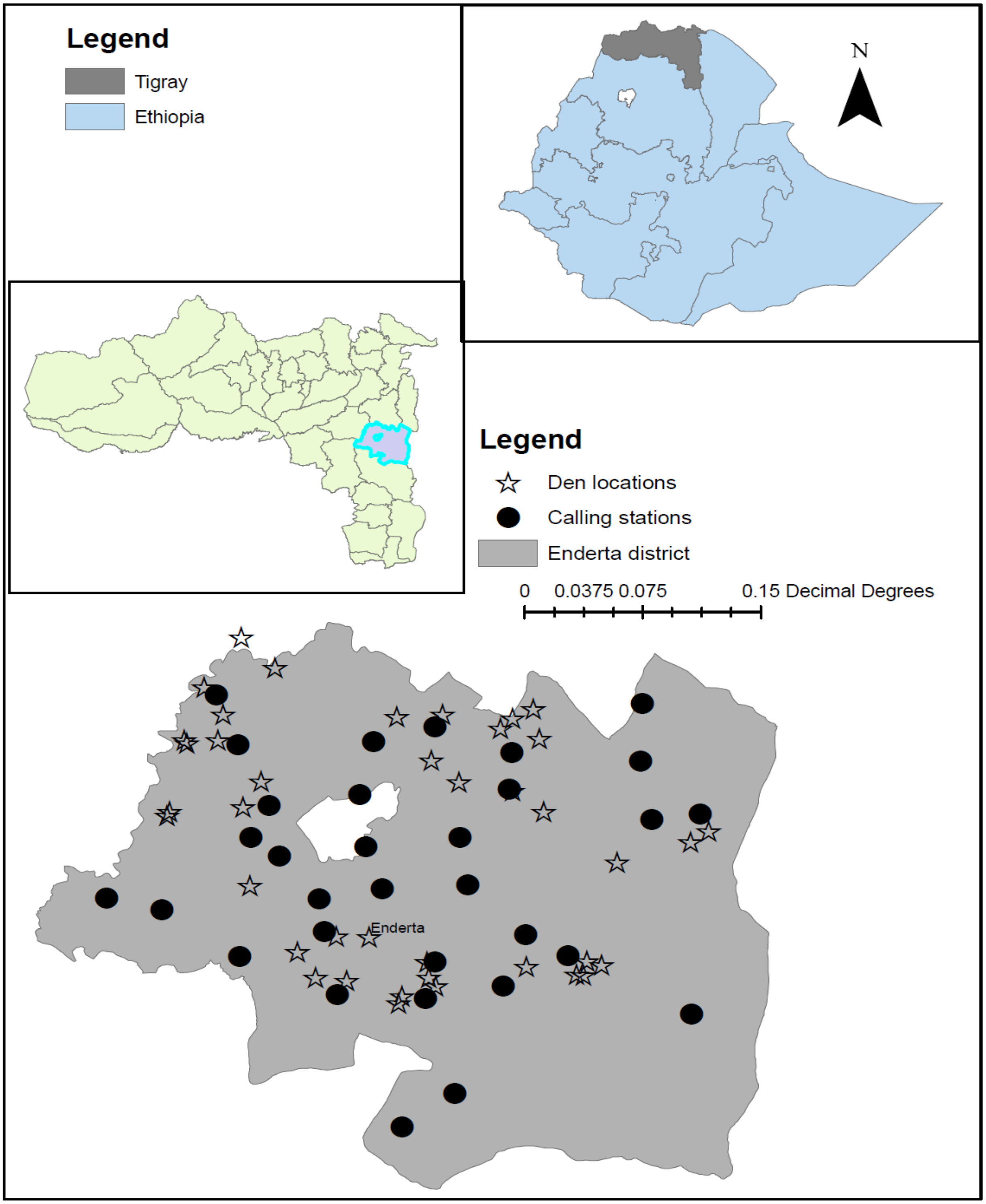

Figure 1 Map of Ethiopia showing the location of Tigray and map of Enderta district showing the locations of calling stations and spotted hyaena dens represented by circles and stars, respectively. The dot highlighted in map of Enderta district represents Mekelle City.

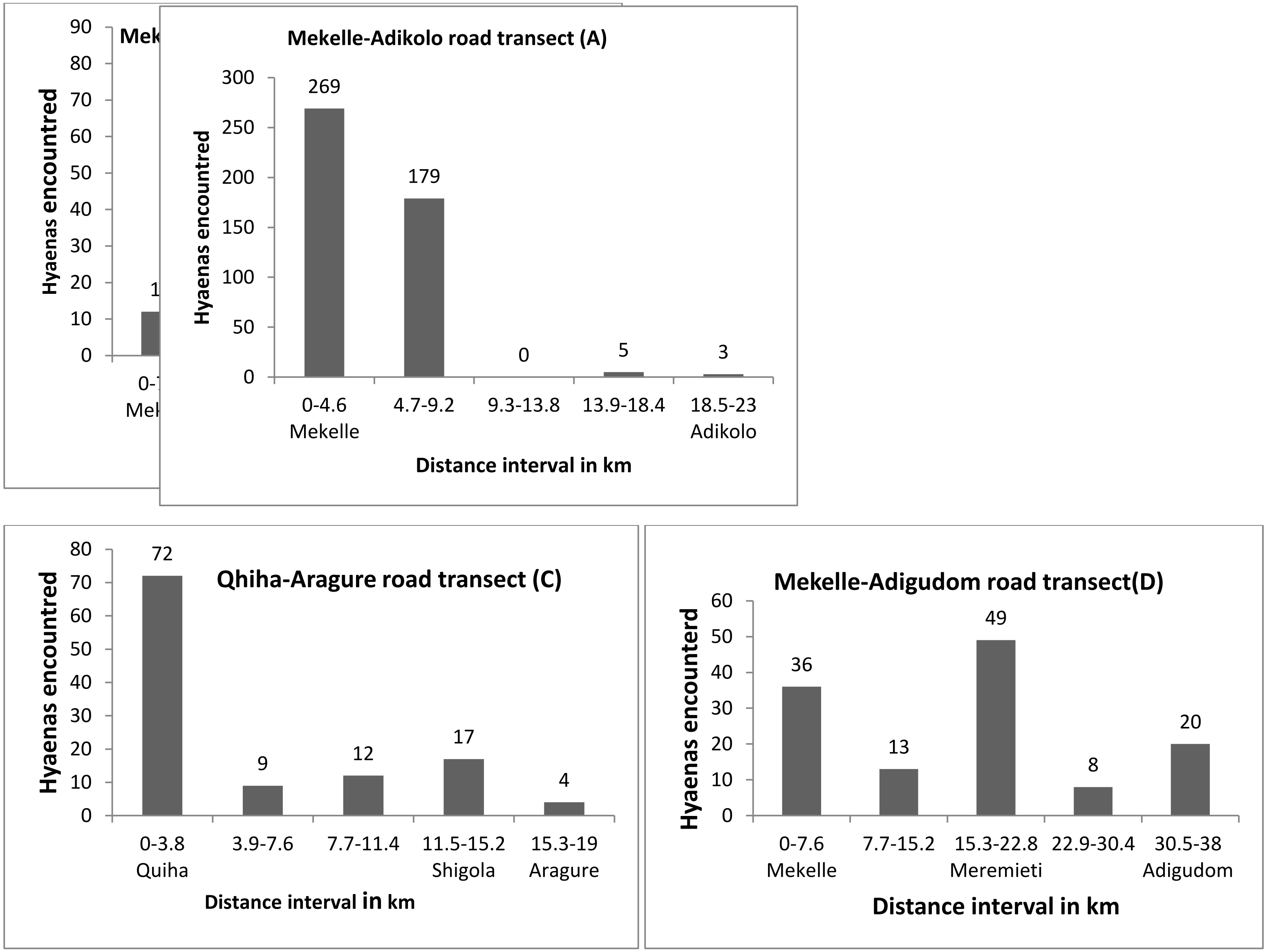
Mekelle-Adikolo road transect (A)
Hyaenas encountred
269
179
0
5
3
0-4.6 Mekelle
4.7-9.2
9.3-13.8
13.9-18.4
18.5-23 Adikolo
Distance interval in km
Qhiha-Aragure road transect (C)
Hyaenas encountred
72
9
12
17
4
0-3.8 Quiha
3.9-7.6
7.7-11.4
11.5-15.2 Shigola
15.3-19 Aragure
Distance interval in km
Mekelle-Adigudom road transect(D)
Hyaenas encounterd
36
13
49
8
20
0-7.6 Mekelle
7.7-15.2
15.3-22.8 Meremieti
22.9-30.4
30.5-38 Adigudom
Distance interval in km

Figure 2 Road transects showing relationship between spotted hyaena and human abundance in northern Ethiopia. Names under the x-axis are towns found in that section of transect, no name means that section was purely rural.

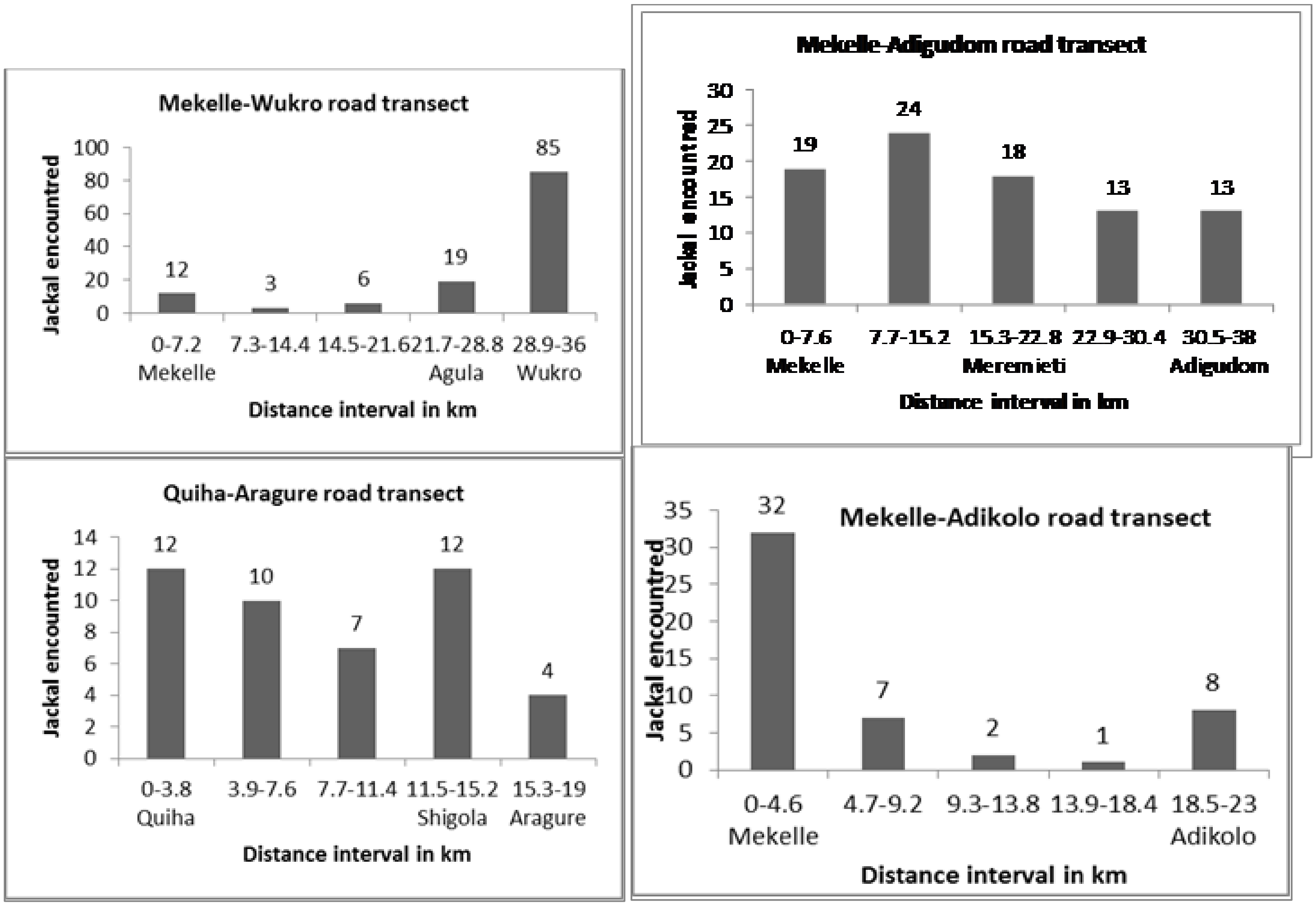

Figure 3 Spatial distribution of golden wolf and human along four road-transects in 2012 in northern Ethiopia. Names under the x-axis are towns found in that section of the transect, no name means that section was purely rural.

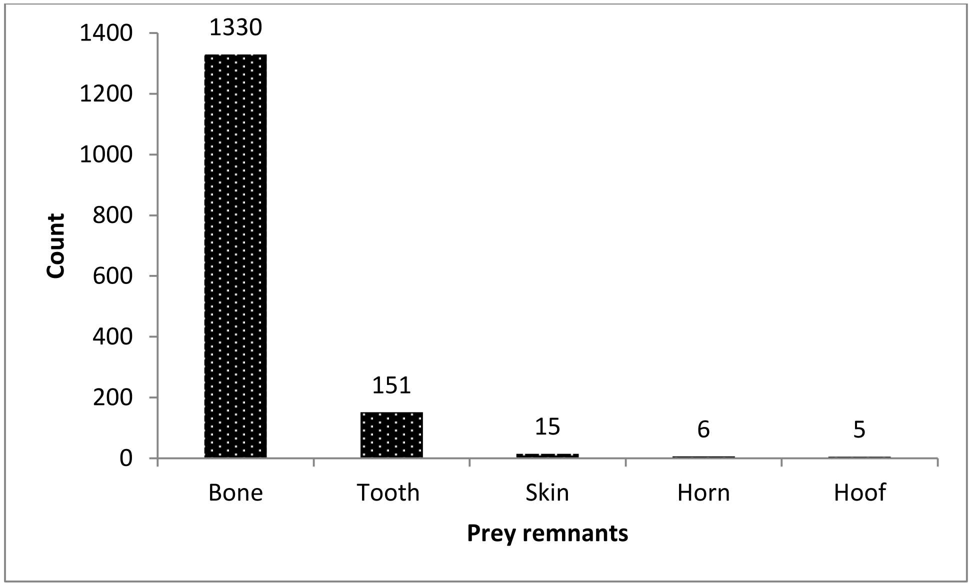

Figure 4 Total prey remnants found at 22 spotted hyaena dens in 2012 in Enderta district, northern Ethiopia

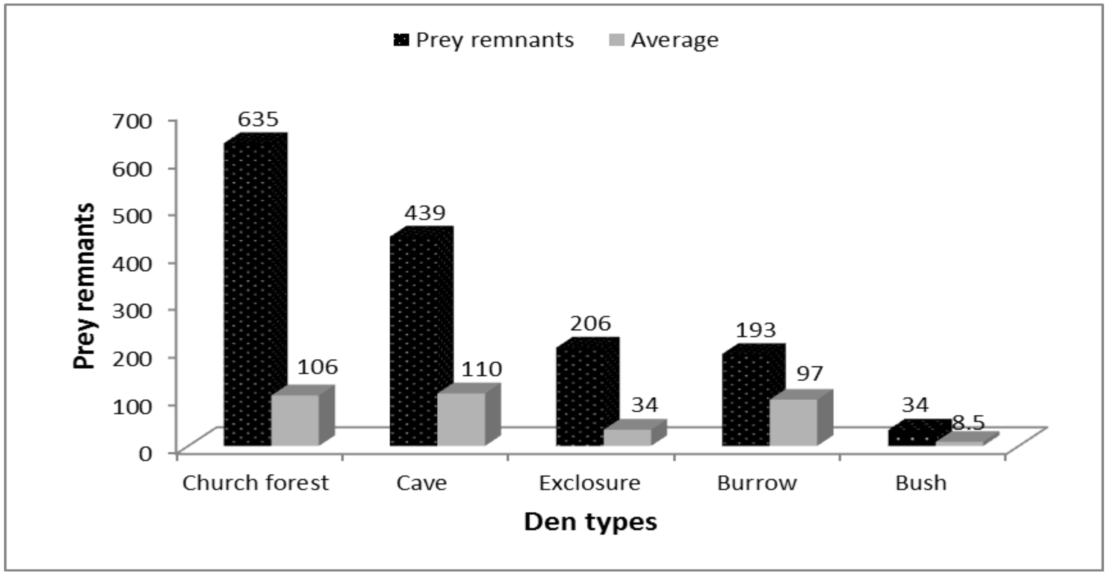

Figure 5 Total and average prey remnants at different spotted hyaena den types (n=22) in 2012 in Enderta district, northern Ethiopia

Table 1 Spotted hyaena and golden wolf counts during wet and dry season in four road-transects in 2012 in Enderta district, northern Ethiopia

Season	Transect	Length in km	Hyaena	Golden wolf	Frequency	Mean viewing distance (in m)
Dry	Mekelle-Adikolo	23	157	25	11	90
	Mekelle-Adigudom	38	86	62	11	96
	Mekelle-Wukro	36	140	96	10	97
	Quiha-Aragure	19	58	32	9	70
	Total		**441**	**215**	**41**	
Wet	Mekelle-Adikolo	23	299	25	10	59
	Mekelle-Adigudom	38	39	25	5	72
	Mekelle-Wukro	36	43	29	4	59
	Quiha-Aragure	19	49	13	6	87
	Total		**430**	**92**	**25**	

* The Frequency column refers to the number of survey nights

Table 2 Number of spotted hyaenas that responded during calibration experiments at various distances from the calling stations in Enderta district, northern Ethiopia

Distance (km)	**Number played to**	**Number responding**	**Response probability**
2	6	3	0.5
2	11	10	0.9
2	1	1	1
2	7	6	0.9
2.3	6	5	0.8
2.5	5	5	1
2.5	15	14	0.9
2.5	3	3	1
2.5	5	4	0.8
2.5	3	3	1
2.6	4	3	0.7
2.8	6	5	0.8
2.8	3	2	0.7
2.8	2	2	1
2.8	6	3	0.5
3	6	0	0
3.5	8	0	0
4	5	0	0

Table 3 The total number of spotted hyaena and golden wolves (*n*) and estimates of the expected number of individuals (μ) in each location, estimated spotted hyaena and golden wolf population size (Ps) and population density (D) (number/km^2) for each of the five locations of calling stations in Enderta district, northern Ethiopia.

		Spotted hyaena					Golden wolf				
Location	**Calling stations**	Area (km^2)	n	μ	Ps	D	Area (km^2)	n	μ	Ps	D
Open agricultural area	20	492.4	198	11.9	239	0.49	392.6	42	2.6	52	0.13
Human settlement	9	221.6	159	21.3	192	0.87	176.7	8	1.1	10	0.06
Area enclosure	2	49.2	49	29.5	59	1.2	39.3	7	4.4	9	0.23
Bushy natural area	2	49.2	6	3.6	7	0.1	39.3	1	0.6	1	0.03
Garbage dumping site	1	24.6	150	181	181	7.4	19.6	5	5	6	0.31
Total	**34**	**837.1**	**562**	**19.9**	**677**	**0.8**	**667.5**	**63**	**2.3**	**79**	**0.12**

*n is the total number of hyaenas and golden wolves that responded in each location of call-ups. μ is the expected number of hyaenas and golden wolves within the response range. Response range and probability for hyaenas and golden wolves were 2.8 and 2.5 km and 0.83 and 0 .8, respectively. $u_s= y_{s/Ss}$ and Ps = n/response probability.*NT = (AH/AS)u where AH =the area of the entire district (1416 km^2) and AS =the area sampled around a call-in station (24.62 km^2 for hyaenas and 19.63 km^2 for golden wolf) and u (19.9 for hyaena and 2.3 for golden wolf) and this gives the final population numbers of spotted hyaena (1,145) and golden wolf (166).

Table 4 Characteristics of spotted hyaena dens (n=40) located in human-dominated landscapes in Enderta district, northern Ethiopia

Items	**Category**	**Count**	**Percentage**
Distance from the nearest town	<=5km	22	55
	6-10km	10	25
	>=11km	8	20
Distance from the nearest hyena den	<=3km	28	70
	>=4km	12	30
Distance from the nearest village	1-2km	34	85
	3-4km	6	15
Distance from the nearest stream	<=1km	25	62.5
	1.5-2km	10	25
	>=3km	5	12.5
Grazing intensity	None	16	40
	Low	6	15
	Medium	0	0
	High	4	10
	Very high	14	35
Human disturbance	None	12	30
	Low	6	15
	Medium	2	5
	High	4	10
	Very high	16	40
Vegetation cover	Low	6	15
	Medium	2	5
	High	3	7.5
	Very high	29	72.5
Habitat	Church forest	11	27.5
	Enclosure	13	32.5
	Caves	6	15
	Bush	7	17.5
	Burrow den	3	7.5
Protection	Safe	35	87.5
	Unsafe	5	12.5
Livestock attack in and around	Yes	36	90
	No	4	10

*Distance was measured by driving from the reference point. Human disturbance and protection of livestock were determined with local people living nearby the dens.