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Behaviour and ecology of the Ethiopian wolf (*Canis simensis*) in a human-dominated landscape outside protected areas

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Abstract

The Ethiopian wolf (*Canis simensis*) is a very rare, endangered, endemic species surviving in isolated mountain pockets in the Ethiopian highlands, with nearly 50% of the global population living outside protected areas. In this paper we compare the ecology and behaviour of an Ethiopian wolf population living in Guassa, a communally managed area in the Central Highlands, with that of the Bale Mountains National Park in the Southern Highlands. Ethiopian wolves live at lower density in Guassa ($0.2 \pm 0.05/\text{km}^2$) than in the Bale Mountains, but giant molerats (*Tachyoryctes macrocephalus*), the main prey for Ethiopian wolves in Bale Mountains, do not occur in the Central Highlands. Faecal analysis identified nine prey categories across wet and dry seasons common to both populations. In total, rodents accounted for 88% of prey volume in wolf diets. Home-range size was positively related to pack size ($r^2 = 0.85$) and there was no difference in mean home-range sizes in both areas. In Guassa, however, wolves spent less time in the presence than in the absence of humans, but wolves spent similar amounts of time in the presence and absence of cattle. These findings suggest wolves can cope with, or adapt to, the presence of livestock and people in communally managed areas.

INTRODUCTION

Wildlife living in human-dominated landscapes has to cope with, or adapt to, the direct or indirect consequences of human activity. Both direct (Hulbert, 1990; Lott & McCoy, 1995) and indirect (Boyle & Samson, 1985; Duffus & Dearden, 1990; Albert & Bowyer, 1991) interactions between humans and wildlife can have a detrimental effect on the survival of a species. The problem is particularly acute for large carnivores, which have extensive home ranges at the top of food chains and which may cause conflicts with humans (Woodroffe & Ginsberg, 1998). Thus, many large carnivores are threatened by habitat destruction, disease and persecution (Treves & Karanth, 2003). As a result, increasingly few large carnivore populations survive outside protected areas.

With a total world population of 500 individuals, the Ethiopian wolf, *Canis simensis*, is the rarest canid in the world and is listed as Endangered by the IUCN (Sillero-Zubiri & Marino, 2004). Ethiopian wolves live in packs, with a discrete social unit that communally shares and defends an exclusive territory. Ethiopian wolves are most active by day and feed almost exclusively upon diurnal small mammals in the high altitude Afro-alpine rodent community, and particularly on the giant molerat (*Tachyoryctes macrocephalus*) in the Bale Mountains. Unlike many carnivores, Ethiopian wolf pack members forage and feed alone (Morris & Malcolm, 1977; Sillero-Zubiri, 1994; Sillero-Zubiri & Gottelli, 1995*a*,*b*; Sillero-Zubiri, Tattersall & Macdonald, 1995*b*). Like other carnivores, the Ethiopian wolf is threatened by habitat destruction, disease, persecution and hybridisation (Sillero-Zubiri & Macdonald, 1997; Haydon, Laurenson & Sillero-Zubiri, 2002; Sillero-Zubiri *et al*., 2004). The ecology and natural history of the Ethiopian wolf in the Bale Mountains National Park (BMNP) in the Southern Highlands of Ethiopia (Fig. 1) is well known as a result of studies conducted from 1988 to 1992 (Sillero-Zubiri & Gottelli, 1995*a*,*b*; Sillero-Zubiri & Macdonald, 1998). Nevertheless, no detailed ecological studies have been carried out to date on other populations of Ethiopian wolves, especially those living in human-dominated landscapes outside protected areas, or of those in other highland blocks in Ethiopia.

There are important ecological differences in the structure of rodent communities between highland blocks in Ethiopia. Some rodent species, particularly the giant

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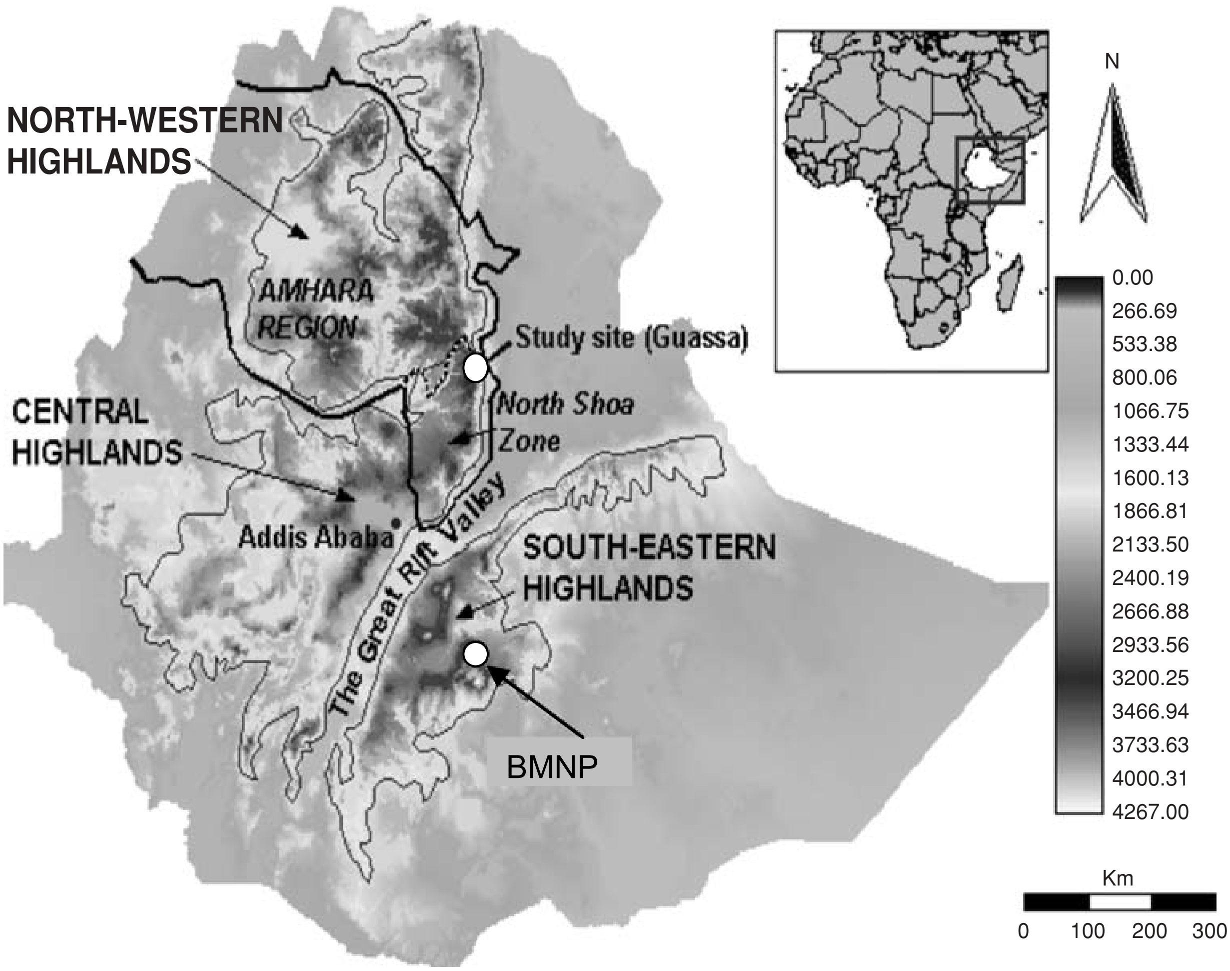

Fig. 1. The highland blocks of Ethiopia and the locations of the Guassa area and the Bale Mountains National Park (BMNP).

molerat that comprises the main prey of wolves in the Bale Mountains, are absent in other highland blocks (Yalden, Largen & Kock, 1976; Yalden *et al*., 1996), which, in turn, may influence wolf ecology. Furthermore, competition from other large carnivores may be either absent or reduced in human-dominated landscapes (Macdonald, 1992), such as in the Central Highlands area of Guassa (Fig. 1). This area has no formal conservation status and supports extensive sanctioned harvesting of grass and firewood and grazing of livestock (Ashenafi, 2001), as well as the second largest known population of Ethiopian wolves outside the protected area system (Marino, 2003).

In order to design more appropriate actions for the future conservation of this threatened canid, it is important to understand the nature and extent of interactions between Ethiopian wolves, humans and livestock. This paper aims to compare the behaviour and social organisation of Ethiopian wolves in the unprotected and human-dominated Central Highlands area of Guassa, with data published previously for the Bale Mountains National Park, where less disturbance might be expected. Specifically, we aim to quantify the feeding ecology, home range and habitat preference of Ethiopian wolves in the Guassa area and to examine possible differences that might arise from the consequences of human activity in the two areas.

STUDY AREA

Guassa (latitude 10° 15′–10° 27′N and longitude 39° 45′–39° 49′E) is situated in an area locally known as Menz (Fig. 1) in the Amhara Regional State of North Shoa, in the central portion of the Ethiopian highland massif. The Guassa range comprises 111 km^2 and lies at an altitude range of 3200 to 3700 m above sea level (a.s.l.). The vegetation of the Guassa area is characterised by high altitude Afro-alpine vegetation: *Euryops–Alchemilla* shrubland, *Festuca* grassland, *Euryops–Festuca* grassland (mima mounds), *Helichrysum–Festuca* grassland and *Erica* heathland are the predominant vegetation communities, while less dominant communities include: *Lobelia–Festuca* grassland, swamp grassland and *Hypericum* shrubland.

The Guassa is managed by the Menz community as a common property resource and is used for livestock grazing and for the collection of firewood and grass. Cattle are the most commonly grazed livestock and usually tend not to be herded. In contrast, sheep occur infrequently, but are herded. The community continues to protect the area by enacting various bye laws, which restrict community use of the natural resources, without any formal protection status (Ashenafi, 2001; Ashenafi & Leader-Williams, in press).

METHODS

Population estimate

Ethiopian wolf density was estimated using the line transect method (Buckland *et al*., 1993). Transects were laid 1 km apart using Universal Transverse Mercator (UTM) gridlines on a 1:50 000 scale map, with the help of a Global Positioning System (GPS). A total of 18 transects covering a total distance of 71 km were laid out across the study area and were walked bi-monthly from December 1996 to November 1998. Data were analysed using DISTANCE 3.5 Release 5. Buckland *et al*. (1993) recommend that the number of sightings should be > 60 for DISTANCE analysis to produce a reliable estimate. Since few wolves were sighted along transects, data from all months were pooled to produce an overall density estimate for the study period.

Faecal sample analysis

A total of 348 faecal samples was collected from January 1997 to December 1998, away from areas of human activity to avoid collecting domestic dog faeces. Samples were air-dried, broken and examined using a hand-held lens. Their contents were sorted and categorised as bones, teeth, hair, bird feathers or vegetable matter, while rodent, sheep and Starck's hare (*Lepus starcki*) remains were identified to species level. The data were described in two ways. First, we calculated the proportion of occurrences of a particular prey item across all samples (Ciucci *et al*., 1996). Second, we calculated the volume of each of certain prey types within each faecal sample, namely: rodents, sheep, Starck's hare, bird feathers and vegetable matter.

Radio-tracking

Five wolves from different packs were trapped in March 1997 using padded leg-hold traps (Sillero-Zubiri, 1996) and fitted with radio-collars (Biotrack, Dorset, UK) weighing 200 g each. The collared animals comprised three females and two males (Asbo (A2♀), Gera (G1♂), Ketema (K2♀), Ras (R2♀) and Murtina (M1♂).

Collared wolves were radio-tracked on foot regularly for 2 years. Once a wolf was located, it was kept in sight for as long as possible and records were taken every 15 min of its location (GPS fix), the group size, its activity, the vegetation height and the habitat type. Pack home range was calculated similarly after identifying pack members individually by using a collared wolf to identify each pack.

Home-range size of radio-collared wolves was analysed using a minimum convex polygon (MCP) method, selected to allow comparison with the Bale Mountains study (Sillero-Zubiri, 1994; Sillero-Zubiri & Gottelli, 1995*b*). The transmitter of one male wolf (M1♂) soon failed (< 5 months) and this wolf was excluded from the analysis of home range due to the small number of fixes (Seaman & Powell, 1996).

Foraging behaviour

The foraging behaviour of individually known wolves was studied during a total of 536 focal watches, with observation periods lasting from < 5–90 min. Individuals were followed on foot and watched from a distance with binoculars. All activities related to feeding and hunting, both successful and unsuccessful, were recorded. Focal watches ended only when the wolf disappeared from sight.

Abundance of prey species

The density of murine rodent prey species in different habitat types was estimated by using live and snap trapping (Ashenafi, 2001). The density of the common molerat, *Tachyoryctes splendens*, was sampled by counting active burrows using a 5 m radius circular plot along transects (Sillero-Zubiri, Tattersall & Macdonald, 1995*a*), while density was estimated following Reid, Hansen & Ward (1966), Jarvis & Sale (1971) and Jarvis (1973).

To determine preference for each rodent prey category, their volume in the diet and their biomass was used to calculate the Chesson index (Chesson, 1978; Vos, 2000):

$$\mu = rn^{-1}\left(\sum_{j=1}^{m} r_j n_j^{-1}\right)^{-1}$$

Where: $r =$ the volume of each prey category in the diet; $n =$ the relative biomass of the same prey category in the area; $m =$ number of prey categories; and the sum of μ across all possible species or prey categories $= 1$. Thus, the larger the values for individual species or prey categories, the more preferred is the prey.

Habitat preferences

The habitat preferences of Ethiopian wolves were calculated by comparing the proportion of time all wolves were sighted in a particular habitat in relation to its total coverage within the study area. All the habitats used by Ethiopian wolves in Guassa are open and unlikely to bias the chances of seeing wolves in particular habitats. We used multiple regression to determine which factors best explained habitat preferences. The densities of rodents in each habitat type and the area of each habitat type in the Guassa area were taken as explanatory variables and the proportion of all wolf sightings within each habitat type was taken as the dependent variable. The quality of Ethiopian wolf habitat was classified on the basis of the biomass of available rodents in each habitat type, following Gottelli & Sillero-Zubiri (1992).

Effects of human and livestock presence on wolf activity

While observing radio-collared wolves, livestock and people were located by scanning from vantage points.

Behavioural data on wolves were collected every 15 min using focal watches (Altmann, 1974), although sometimes wolves moved quickly from view. Data collected included location (GPS fix), activity, presence and absence of humans and of livestock, distance from humans and livestock (estimated to nearest 50 m) and response to presence of humans and livestock. This latter was classified as one of: alarm call, a high-pitched bark followed by trotting or running away from humans; move away, moving slowly away from the area; aware, showing regular vigilance while continuing to perform its normal activity; ignore, when the wolf did not respond to human presence.

Wolf responses were analysed separately for human and livestock presence, using a chi-square test and a Generalised Liner Model (GLM) with normal error structure. GLM was used to estimate the effects of human and livestock presence on the length of time a wolf performed a given activity. The length of effective observation time was taken as the dependent variable. Two independent categorical variables, comprising presence and absence of humans or livestock and the different categories of wolf activities (a categorical variable with 5 levels) and their relationship were fitted in the model.

RESULTS

Population estimate

The density of Ethiopian wolves in the Guassa area was estimated as $0.2 \pm 0.05/\text{km}^2$. Based on the total area of the Guassa, the total population estimate of Ethiopian wolves in Guassa was 21 ± 5 individuals. No other carnivores, neither spotted hyaenas (*Crocuta crocuta*) nor domestic dogs, were seen along the transects.

Diet

Nine categories of prey item were found in wolf faeces from Guassa and there was no seasonal difference in the frequency of prey items between the wet and dry seasons ($\chi^2 = 0.516$, d.f. $= 8$, $P > 0.05$). Therefore, data for both seasons were combined. Rodents were the most important prey in terms of frequency of occurrence and total volume (88.1%). Murine rodents were present in 94.5% of samples and accounted for 71.5% by volume. *Arvicanthis abyssinicus* and *Lophuromys flavopunctatus* were the most common diurnal murine rodent species in faeces, while the nocturnal *Stenocephalemys griseicauda* was the least common murine rodent. The fossorial common molerat, *Tachyoryctes splendens*, was present in 30.6% of samples and accounted for 16.6% by volume. Sheep's wool and hair from Starck's hares, *Lepus starcki*, were present in 7.5% and 10.6% of faecal samples and accounted for 4.1% and 5.8% by volume, respectively. Bird feathers and grass were present only infrequently (Table 1).

Table 1. Prey items of Ethiopian wolves from 348 faecal samples collected in the Guassa area, shown as frequency of occurrence within the total sample and volume across the whole sample

Prey category and rodent species	Frequency of occurrence *n*	(%)	Volume (%)
Murine rodent (bone, teeth and hair)	455	94.5	71.5
Arvicanthis abyssinicus	207	59.5	32.5
Lophuromys flavopunctatus	148	42.5	23.2
Otomys typus	89	25.6	14.1
Stenocephalemys griseicauda	11	3.1	1.7
Molerat (bone, teeth and hair)			
Tachyoryctes splendens	106	30.6	16.6
Starck's hare *Lepus starcki* (hair)	26	7.5	4.1
Sheep's wool	37	10.6	5.8
Bird feathers	6	1.72	0.9
Vegetable matter (grass)	7	2.01	1.1

Foraging behaviour

Wolves spent 67.5% of daylight hours foraging. Prey was stalked over periods lasting from a few minutes to 20 min, with a mean of 9.5 ± 2.7 min ($n = 219$). Wolves were successful in catching small murine rodents on 57.1% of stalking attempts. Digging is the favoured way of catching the common molerat, *T. splendens*, and 21.0% of digging attempts ($n = 89$) were successful. While the Ethiopian wolf in Guassa primarily feeds on live rodents, stalking of Starck's hares, *L. starcki*, and feeding on carrion, accounted for 3.4% ($n = 9$) of their foraging activity.

The density and biomass of these rodents in the three main habitats (*Euryops–Alchemilla*, *Festuca* and 'mima' mounds) was estimated using multiple-capture live trap data (Table 2). The density of the common molerat was

Table 2. Biomass (kg/km^2) of three diurnal rodents in the Guassa area

Habitat	*Arvicanthis abyssinicus*	*Lophuromys flavopunctatus*	*Otomys typus*	Total biomass
Euryops–Alchemilla shrubland	571.4	385.8	117.1	1074.3
Festuca grassland	297.1	227.3	179.9	703.4
Mima mound	169.7	317.6	84.6	571.9
Total	1038.2	930.1	381.6	2349.6

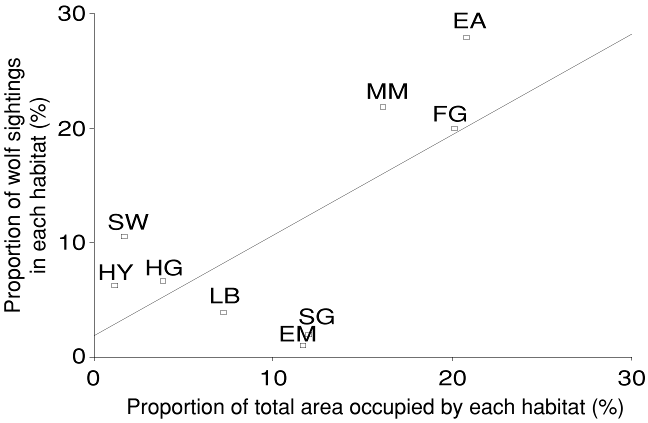

Fig. 2. The relationship between the proportion of time a wolf was found in a particular habitat and the proportion of the total area covered by each habitat. Habitat key: EA, *Euryops-Alchemilla* shrubland; EM, *Erica* moorland; FG, *Festuca* grassland; HG, *Helichrysum-Festuca* grassland; MM, 'mima' mounds; SW, Swamp grassland; SG, Short grassland; HY, *Hypericum* shrubland; LB, *Lobielia-Festuca* grassland.

found to be 786 kg/km^2 in the Guassa area, based on 360 circular sample plots. The relative abundance of the common molerat was highest in *Euryops–Alchemilla* shrubland (24.7%), Mima mound (20.5%) and *Festuca* grassland (19.7%).

Arvicanthis abyssinicus and *O. typus* were the most preferred prey items, with a Chesson index value of 0.3 each. *Tachyoryctes splendens* and *L. flavopunctatus* were the next most preferred prey items, with a Chesson index value of 0.2 each. The nocturnal *S. griseicauda* was the least preferred species among the rodents with a Chesson index value of 0.02.

Habitat preference

Wolves were mostly (70.2% out of 536 sightings) seen in three habitat types, namely: *Euryops–Alchemilla* shrubland, 'mima' mounds and *Festuca* grassland. These three habitats accounted for 61.2% of the total area of Guassa and contained the highest densities of rodents. In contrast, 21.3% of wolf sightings were in swamp grassland, *Helicrysum–Festuca* grassland, *Hypericum* shrubland and *Lobelia–Festuca* grassland, which together accounted for 17.3% of the Guassa area. Finally, *Erica* heathland and short grassland areas accounted for 2.8% of the wolf sightings, while their total area covered 21.3% of the Guassa area.

There was a positive relationship ($r^2 = 0.63$, $F_{1,7} = 11.98$, $P < 0.01$) between the proportion of time Ethiopian wolves spent in a particular habitat and the proportion covered by each habitat (Fig. 2). Points above the regression line indicate that wolves preferred swamp grassland (1.5), 'mima' mounds (1.4), *Euryops–Alchemilla* shrubland (1.3) and *Festuca* grassland (1.1) over other habitat types. Short grassland (0.2) and *Erica* moorland (0.01) were the least preferred habitats. However, a multiple regression using the proportion of sightings as the dependent variable and the proportional habitat size and rodent density as explanatory variables, showed that the only predictor of wolf habitat preference was the density of rodents ($F_{1,4} = 27.49$, $P < 0.01$) in a model that explained 87.3% of the variance.

Group size and home range

The four packs, (Asbo, Dija, Ras and Gera) each comprised between 4–9 adults and sub-adults (> 1 year old) with a mean pack size of 5.7 ± 0.25 individuals. The mean annual home range of four radio-collared wolves was 6.37 ± 0.4 km^2. Home-range size differed between individuals ($\chi^2 = 15.7$, d.f. = 3, $P < 0.01$). The combined home ranges for all members of each of the four packs ranged from 5.5–9.2 km^2, with a mean pack home range size of 7.2 ± 0.8 km^2. Home ranges of adult and sub-adult wolves overlapped almost completely with other pack members. A comparison of home-range size to pack size suggested a positive relationship between the size of home range and pack size ($r^2 = 0.85$), but the relationship was not significant ($F_{1,3} = 4.98$, $P > 0.05$) for this small sample size.

Effect of human presence on wolf activity

On most occasions when Ethiopian wolves were recorded close to people collecting grass or firewood, they were at distances of between > 50 m and < 150 m (Fig. 3). In most cases, wolves moved away slowly from people, but they also frequently ignored human presence. Wolves less frequently remained aware of people or made an alarm call.

There was no difference between the proportion of time spent foraging in the presence and absence of people ($\chi^2 = 2.45$ d.f. = 1, $P > 0.05$). However, wolves tended to lie down more when people were not in the area ($\chi^2 = 21.62$, d.f. = 1, $P < 0.001$). In contrast, wolves ran more when humans were in the area ($\chi^2 = 12.2$, d.f. = 1, $P < 0.001$). In most cases when the wolf was recorded as walking (55.5%), the wolf was already moving away from the advancing humans.

There was no relationship ($\chi^2 = 11.48$, d.f. = 12, $P > 0.5$) between the different activities of wolves in relation to distance from humans. However, the proportion of activities such as foraging and walking tended to increase as distance from humans increased, while running away from humans tended to decrease as distance increased (Fig. 3).

Overall, wolves spent less time in the presence, than in the absence, of humans ($F_{1,441} = 5.77$, $P < 0.05$). A Tukey analysis indicated that there was no difference between mean time spent foraging ($P > 0.05$), walking ($P > 0.05$) and running ($P > 0.5$) in the presence or absence of humans. However, a difference was evident between standing and lying when humans were present and absent ($P < 0.05$).

There was no relationship ($F_{4,403} = 1.68$, $P > 0.05$) between the length of time an activity was performed in the presence or absence of people, in a model that explained

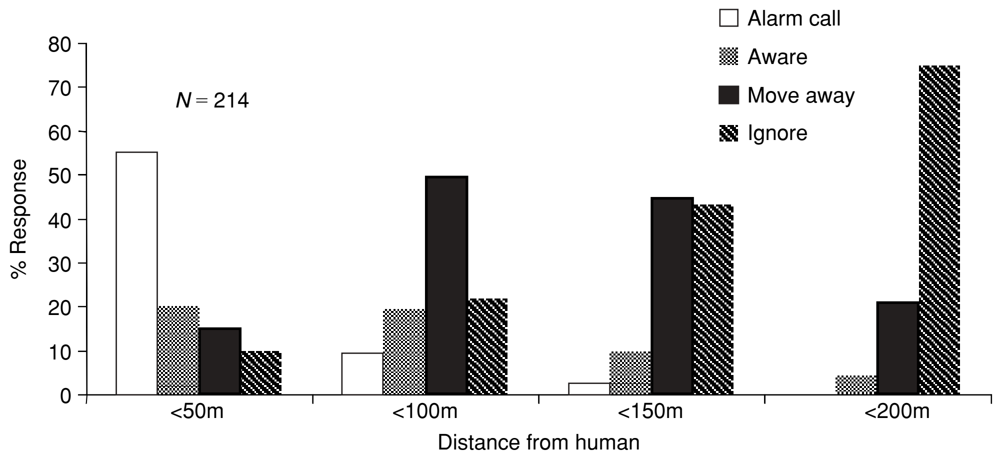

Fig. 3. Proportions of different responses by the Ethiopian wolf in relation to distance from humans.

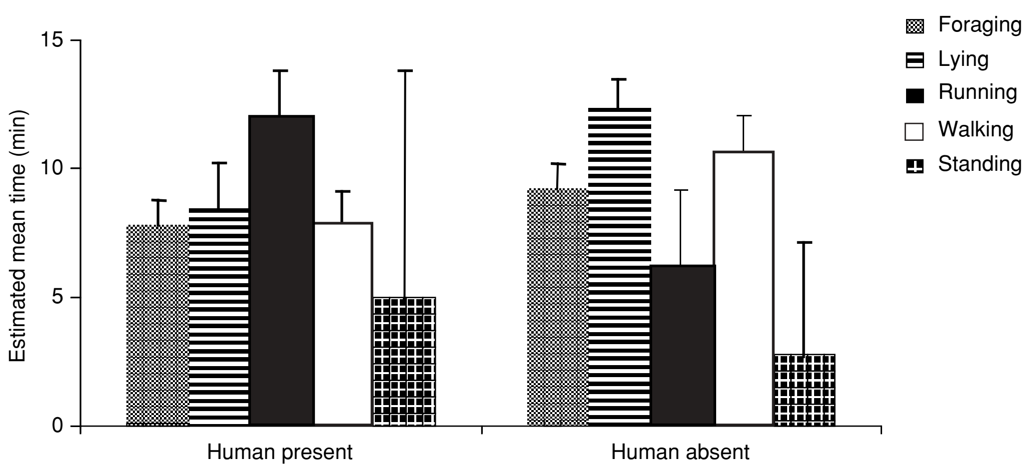

Fig. 4. Estimated mean length of time for each activity during human presence and absence from the GLM.

61.0% of the variance (Fig. 4). This suggests that there was little or no influence of human presence or absence on different activities of the wolf.

Effect of livestock presence on wolf activity

Very few interactions were observed between Ethiopian wolves and sheep herds. On most occasions when wolves were recorded close to livestock, this was usually to cattle at distances of between > 50 m and < 200 m. Wolves did not respond to cattle as they did to people collecting grass and firewood, but largely continued with their prevailing activities. Indeed, wolf activity differed ($\chi^2 = 14.53$, d.f. = 4, $P < 0.05$) in the presence and absence of cattle and more foraging activity took place in the presence of cattle.

There was no difference in the time that wolves were observed in the presence and absence of livestock ($F_{7,415} = 1.51$, $P > 0.05$). There was also no relationship ($F_{5,419} = 2.45$, $P > 0.05$) between the length of time an activity was performed in the presence or absence of livestock in a model that explained only 31.0% of the deviation (Fig. 5). This suggests that there was little or no influence of livestock presence on different activities of the Ethiopian wolves.

DISCUSSION

Over 50% of the total population of the world's rarest canid species lives outside protected areas (Marino, 2003), yet this is the first study of the behaviour and ecology of Ethiopian wolves living in an unprotected and human-dominated landscape. Despite the exploitation of natural resources by local people, the ecology of wolves in the Guassa area is similar to that in the Bale Mountains National Park, which has remained relatively undisturbed, at least until the early 1990s (Sillero-Zubiri & Macdonald, 1997; Stephens *et al.*, 2001). Even though the giant molerat does not occur in the Central Highlands (Yalden, 1985; Yalden *et al.*, 1996), Ethiopian wolves remain rodent specialists in Guassa and depend on murine rodents and the common molerat. The home range and social organisation of Ethiopian wolves in Guassa is similar to that in the Bale Mountains, but their current density is lower in Guassa than in the Bale Mountains.

The global range of the Ethiopian wolf comprises 11 small areas of Afro-alpine habitat, of which the largest is the Bale Mountains, while nine of these areas are outside protected areas, including the Guassa area of Menz (Malcolm & Tefera, 1997; Marino, 2003). The density of wolves in the Guassa area was estimated to

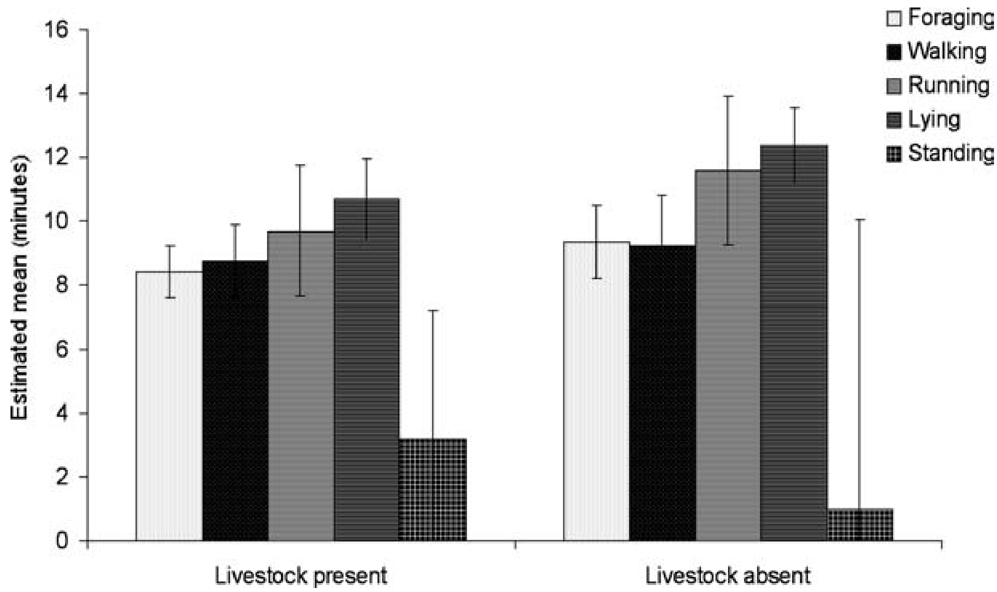

Fig. 5. Estimated mean length of time for each activity during livestock present and absent from the GLM.

be 0.2/km^2, which is lower than the recent estimate of 0.5/km^2 for prime habitats in the Bale Mountains National Park, but similar to the estimate of 0.2/km^2 for the Simen Mountains National Park (Marino, 2003). Thus, the Guassa and other similar outlying areas are of great importance for the future conservation of the Ethiopian wolf, given that maintaining only one larger population in the Bale Mountains is not ideal (Caughley, 1994; Gottelli *et al*., 1994, 2004; Wayne & Gottelli, 1997).

Ethiopian wolves occupy all three main habitats in the Guassa area. However, habitat preference indices indicate that mima mounds were the most preferred habitat, followed by *Euryops–Alchemilla* shrubland and *Festuca* grassland. The densities of rodents in different habitats largely explain these differences in habitat preference. Similar results have been observed in the Bale Mountains, where wolf density has been positively correlated with diurnal rodent density and negatively correlated with vegetation height (Sillero-Zubiri & Gottelli, 1995*a*,*b*). However, wolves in the Guassa area feed mostly on smaller rodents that do not need to be dug out of deep burrows. In contrast, wolves in the Bale Mountains spend more time digging deeply for their prey, and giant molerats, in turn, make up a greater proportion of their diet (Morris & Malcolm, 1977; Sillero-Zubiri & Gottelli, 1995*a*; Sillero-Zubiri *et al*., 1995*a*,*b*; Malcolm, 1997). Furthermore, there is a much higher biomass of molerats on upland areas of prime habitats in Bale (Sillero-Zubiri *et al*., 1995*b*) than there are of surface-living rodents on lower-lying areas of Bale and in the Guassa area. Hence, this may explain the lower densities of wolves in Guassa and other areas in the Central and North-Western Highlands (Marino, 2003). Nevertheless, there was no difference ($F_{2,10} = 0.71$, $P > 0.05$) in mean pack home-range size of wolves in Guassa and the Web Valley (6.5 ± 2.1 km^2) and Sanetti (5.5 ± 1.3 km^2) packs in the Bale Mountains.

Empirical studies on the effects of disturbance on wild canids are surprisingly uncommon. Nevertheless, it is important that the relationship between the cause and effects of disturbance is understood for the future management of endangered species (Anderson, 1988). For example, populations of grey wolves, *Canis lupus*, in Minnesota are recovering in areas of high human activity (Mech, 1999), but in southern Europe they may avoid diurnal activity to minimise contact with people (Vilá Vicente & Castroviejo, 1995; Ciucci *et al*., 1997). In this study, Ethiopian wolves do show alarm responses when at close distances to people, but not to cattle. The activities of wolves changed very little in the presence of humans or cattle. Most observed associations are with cattle. Ethiopian wolves in Guassa associate with cattle as long as cattle herders do not chase them. In contrast, the few sheep flocks encountered are closely guarded and wolves are invariably chased away.

Ethiopian wolves have also been seen to hunt prey in the presence of people and cattle. Indeed, some wolves were observed to benefit from grazing livestock, which provide a mobile hide from which to hunt for rodents. Such tolerance, and indeed commensalism, may have arisen through habituation as a survival strategy by wolves in human-dominated landscapes. However, some wolves continue to avoid the presence of people and are apparently unable to habituate. Such intolerance of disturbance may be cumulative, as the frequency of disturbance will increase in seasons when the area is most used by people and livestock. Animals may compensate for an energy loss due to disturbance if their time budget is not limiting (Stockwell, Bateman & Berge, 1991). However, a species like the Ethiopian wolf, that subsists on small rodents and spends most of the day feeding to meet its daily metabolic requirements, may face serious constraints from disturbance and may have to use an effective strategy to cope with human and livestock disturbance. Additional compensatory activity may have an important influence on the total time budget of the Ethiopian wolf in human-dominated landscapes outside protected areas and this could include foraging at night or feeding more on carrion. However, wolves in Guassa did not hunt at night, but there was more evidence of wolves scavenging in Guassa than in the Bale Mountains.

The availability of food can affect the intensity and pattern of human disturbance on various colonies of birds (Anderson, Gress & Mais, 1982; Van der Zande & Verstrael, 1985). However, there is little evidence to suggest that the presence of human and cattle affects the foraging activities of wolves in the Guassa area. Equally, an important assumption is that the relationship between disturbance level and responses, whether negative or positive, is a matter of degree. In other words, that there is a graded effect where a range of disturbance levels exist (Anderson, 1988). A minimum effective level of disturbance is a reality in human-dominated landscapes. It follows then, that some kind of safe or acceptable level of disturbance should be estimated. It is important in the management and conservation of endangered species to quantify the level and effect of disturbance, so that causes of disturbance can be identified and their negative impact can be eliminated or mitigated.

It is important to document the degree of adaptability of Ethiopian wolves in a human-dominated landscape, because resource managers may face decisions about whether or not to place land-use restrictions in areas where wolves occur outside protected areas. However, land-use restrictions are highly controversial, particularly when people obtain resources from Ethiopian wolf ranges and where many local residents might further oppose or resent wolves as a result of such restrictions.

Therefore, in areas where national parks are unlikely to be economically viable or socially desirable, an alternative approach is required. Community-led conservation initiatives are one possible approach. Their eventual success requires both an understanding of the varying components of the ecosystem and of the interaction between the indigenous population and the resources upon which they depend.

In conclusion, this paper has shown that a population of Ethiopian wolves, important to the long-term survival of one of the world's most threatened canids, has persisted in the formally unprotected Guassa area and has coped with, or adapted to, human disturbances. Furthermore, the key habitats upon which the wolf and its prey depend have been conserved under an effective indigenous common property resource management system. This conservation of critical habitat has been achieved by full community participation and without investing in protected area budgets or by interfering with the existing land use by the human community, while at the same time conserving important and threatened biodiversity, including this important population of Ethiopian wolves (Ashenafi, 2001; Ashenafi & Leader-Williams, in press).

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