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Ecology and conservation of spotted hyena (*Crocuta crocuta* Erxleben 1777) in human dominated landscapes in Northern Ethiopia
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1

General Introduction

1.1 Carnivore conservation

Human activities have caused a decline in carnivore populations worldwide (Woodroffe, 2000). Conservation of large carnivores is very challenging due to expanding human populations and their associated impacts. These challenges are particularly acute in sub-Saharan Africa, where there is a rapid increase in human populations (Ceballos & Ehrlich, 2006). In this region, the rising demand for agriculture and husbandry (Mearns, 1997) results in land degradation and habitat fragmentation. Carnivores are declining very rapidly in some regions due to loss of habitat, depletion of prey, hunting, diseases and trade in body parts as well as conflict with humans (Novaro et al., 2000; Sillero-Zubiri & Laurenson, 2001). Habitat fragmentation and persecution by humans is linked to the disappearance of large carnivores such as wild dogs (*Lycaon pictus*, Temminck, 1820), cheetahs (*Acinonyx jubatus*, Schreber, 1775), lions (*Panthera leo*, L. 1758) (Woodroffe, 2001; Ogada et al., 2003; Patterson et al., 2004; Packer et al., 2005) and spotted hyenas (*Crocuta crocuta*) (Woodroffe, 2001; Treves & Karanth, 2003; Kolowski & Holekamp, 2006; Kissui, 2008). Spotted hyenas (*Crocuta crocuta* Erxleben 1777), here after referred as hyenas, experience declines outside of protected areas due to habitat loss and poaching (Honer et al., 2008).

In Western Europe, hyena's extinction coincided with a decline in grasslands 12,500 years ago (Stiner, 2004). Around that time, hyenas were out-competed by wolves and humans when the grasslands favored by hyenas became depleted. Populations of hyenas began to shrink and disappeared completely from Western Europe between 14,000 and 11,000 years ago (Stiner, 2004). Habitat and prey loss may explain the hyena's eventual disappearance not only from Europe but Asia as well (Stiner, 2004).

Persecution can reduce the population size of large carnivores, including hyenas (Woodroffe, 2001). This often represents a leading source of mortal-

ity (Woodroffe & Ginsberg, 2000) and is often associated with human-carnivore conflicts (Woodroffe, 2000; Ogutu et al., 2005; Johnson et al., 2006). For example, in some areas of Africa farmers may saturate a goat or cow carcass with fast-acting poison, leave this out for hyenas to feed on during the night and in this way kill numerous hyenas simultaneously (Holekamp & Smale, 1992). This kind of mass poisoning as retaliation for livestock depredation has been documented for hyenas in eastern Africa, but it may also occur in the rest of Africa (Holekamp & Smale, 1992).

Large carnivores are usually at the top of food chain and are always present in low densities (Van Orsdol et al., 1985; Hemson, 2003; Loveridge et al., 2007; Croes et al., 2011). They will always be less abundant than their herbivore prey and therefore be more vulnerable to extinction (Noss et al., 1996; Sillero-Zubiri & Laurenson, 2001). Large carnivores have a high propensity for conflict with humans. They have extensive home ranges and need large prey populations to survive, and therefore only large areas can support viable populations (Msuha, 2009). Coexistence between large carnivores and local communities is almost impossible in human-dominated landscapes (Woodroffe & Ginsberg, 2000); they need extensive areas with few people (Lindsey et al., 2013). It is difficult to maintain such ecosystems mainly because of human population growth and the associated demand for land and other resources (Msuha, 2009). As a consequence, large carnivores tend to suffer when human populations expand into intact habitats (Woodroffe & Ginsberg, 1998; Woodroffe, 2000; Sillero-Zubiri & Laurenson, 2001). Retaliatory killing as a cause of mortality is probably more important in Africa, where large carnivores are more abundant and where management may be ineffective because of a lack of sufficient financial and human capacity, than in developed countries (Msuha, 2009).

Low species population density, small geographical range size, long gestation period and high trophic level are factors associated with high extinction risk in carnivores (Cardillo et al., 2004). Moreover, survival of large carnivores depends on their level of conflict with human interests and their social acceptability to humans, particularly outside protected areas (Linnell et al., 2001; Kleiven et al., 2004; Lindsey et al., 2005; Tumenta et al., 2010). Conflict-related mortality can be very high (Woodroffe & Ginsberg, 1998; Macdonald & Sillero-Zubiri, 2002; Kolowski & Holekamp, 2006).

Most of Africa's protected areas are too small to conserve viable populations of large, wide-ranging carnivores (EWCA, 2012a). Such species must utilize adjacent dispersal areas to obtain supplementary food (Woodroffe &

Frank, 2005). There are many designated protected areas of land, including National Parks, Wildlife Reserves, Biosphere Reserves, Priority Forests and Community Conservation Areas in Ethiopia (Young, 2012). However, these protected areas are severely degraded (Young, 2012). Protected grasslands are used for livestock grazing and timber is used for fuel and construction (Young, 2012). Land is being converted for subsistence and commercial agriculture. The primary goal of the Ethiopian Government is poverty alleviation through food production and investment policies (Young, 2012). There is limited and only imprecise information on the status and distribution of large carnivores in Ethiopia (EWCA, 2012a; EWCA, 2012b). Non-protected areas play a vital role in maintaining the existence of carnivores, both in order to increase population size and to allow greater genetic exchange between populations (Linnell et al., 2001; Treves & Karanth, 2003).

As suggested above, most scientific literature on hyena-human interactions in Africa suggests conflict situations, often resulting in the killing of hyenas (Woodroffe, 2001; Treves & Karanth, 2003; Kolowski & Holekamp, 2006; Kissui, 2008). The present dissertation will present an exceptional case of peaceful coexistence between hyena and humans. A high density of hyenas persists peacefully with dense human habitations in non-protected areas in northern Ethiopia. Hyenas are highly adapted to dense human habitations, and their survival is dependent on anthropogenic food (Yirga et al., 2012a). The main objective of this research is to study the ecology and behavior of hyena in a human-dominated landscape in northern Ethiopia.

1.2 Ecology of hyena

1.2.1 Distribution and status

Hyena has a remarkable behavioral plasticity that facilitates its adaptive adjustment to an increasingly precarious lifestyle in proximity to humans (Woodroffe, 2000; Sunquist & Sunquist, 2001; Boydston et al., 2003). They can be nocturnal or diurnal and breed at any time of the year (Van Meter et al., 2009). Hyenas inhabit very wide historical range with relatively stable populations and this shows that hyenas have high behavioral and ecological plasticity (Kolowski & Holekamp, 2009). During the Pleistocene era, hyenas inhabited large parts of Eurasia but currently occur only in Africa (Kurtén, 1968; Werdelin & Solounias, 1991). Hyenas are large (45-80 kg), gregarious carnivores that occur throughout sub-Saharan Africa except for true deserts and alpine areas above 3000 m (Mills, 1990; Frank et al., 1995; Mills &

Harvey, 2001). Hyenas are also generally absent from tropical rainforests, except for Odzala National Park in Congo (Wilson & Reeder, 1993; Ray et al., 2005). Their large range may be due to the hyena's versatile choice of prey, as its food is known to vary across ecosystems (Mills & Hofer, 1998). In Central Africa, the hyena has mainly been reported to inhabit savannahs (Mills & Hofer, 1998; IUCN, 2008), although hyenas have been reported in Odzala National Park, Congo. There have not been recent records inside Algeria, Djibouti, Egypt, Equatorial Guinea, Gabon, Gambia and Liberia. The current distribution of hyenas is limited to Ethiopia, Kenya, Tanzania, Botswana, Namibia, South Africa, Angola, Benin, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Congo, Ivory Coast, Democratic Republic of Congo, Ghana, Lesotho, Guinea Bissau, Malawi, Mali, Mauritania, Mozambique, Niger, Nigeria, Rwanda, Senegal, Somalia and Sierra Leone (Mills & Hofer, 1998).

A tentative estimate of the total population of hyena in Africa is between 27,000 and 47,000 (Mills & Hofer, 1998), which is most likely to be an underestimate. The largest known populations occur in the Serengeti ecosystem, Tanzania and the Kruger National Park, South Africa with estimates of 8,700 and 3,900 hyenas, respectively (Mills & Hofer, 1998). Most hyena populations in protected areas of southern Africa are stable but in protected areas of eastern and western Africa they are declining due to incidental snaring and poisoning (Mills & Hofer, 1998; Craigie et al., 2010). Diseases, habitat loss and persecution by humans make hyenas dependent on conservation areas (Mills & Hofer, 1998).

1.2.2 Feeding habits

Hyena is an opportunistic carnivore, foraging on locally abundant prey species (Cooper et al., 1999). Hyena densities are usually positively correlated with prey biomass densities (Ogutu et al., 2005). The most common prey species include various antelopes (such as *Cephalophus dorsalis*, *Cephalophus niger*, and *Tragelaphus strepsiceros*), zebra (*Equus spp.*), buffalo (*Syncerus caffer*) and juvenile rhinos (*Diceros bicornis*), hippos (*Hippopotamus amphibius*) and giraffes (*Giraffa camelopardalis*) (Mills & Hofer, 1998; Hayward, 2006). Hyenas kill and scavenge on small, medium and large-sized species (Kruuk, 1972; Salnicki et al., 2001). Hyenas detect their prey by sight, sound and smell. They find carrion by the sound of other carnivores feeding, by distress calls, by smell, or during day light hours by watching vultures descend on carcasses (Mills & Hofer, 1998). They are able to hear noises coming from predators killing prey or feeding on carcasses over dis-

tances of up to 10 km (Mills, 1990). An analysis of 14 published studies and one unpublished study about the diet of hyenas throughout their range in Africa was used by Hayward (2006) to establish prey preference and avoidance of large carnivores, including the hyena. He concluded that hyenas do not have a significant preference for a particular prey species. Hyenas eat almost any mammal, bird, fish or reptile, irrespective of size or species (Mills, 1990; Henschel & Skinner, 1990; Sillero-Zubiri & Gottelli, 1992; Salnicki et al., 2001). They have a reputation for killing and scavenging domestic livestock, mostly cattle, sheep and goats, but also poultry, cats, dogs, horses, donkeys, and camels (Mills & Hofer, 1998; Abay et al., 2011; Sogbohossou et al., 2011). Hyenas are opportunistic scavengers of human waste, bones, and dung, and may forage on anthrax-infested carcasses without detrimental consequences. They are capable of eating and digesting all parts of their prey except hair and hooves (Smith & Holekamp, 2010). Hyenas can totally digest bones and only the inorganic components are excreted in their droppings (Smith & Holekamp, 2010). Hyenas are known to be most active during the night (Kruuk, 1972; Mills, 1990). They are flexible hunters, cooperating to bring down larger prey, but foraging alone for smaller animals (Kruuk, 1966) up to 75% of the time (Holekamp et al., 1997). They feed with remarkable speed, 18 kg food per hour (Kruuk, 1972), compared to lions (Kolowski et al., 2007). Hyenas can travel over vast distances. For example, Kolowski et al. (2007) showed that hyena from the Maasai Mara travel on average 12.4 km per night. Length of travel is thought to be dependent on home range size and prey availability.

Ranging behavior of hyenas is typically, but not always, nocturnal, with individuals often moving long distances when active (Kruuk, 1972; Mills, 1990). Previous studies have shown that onset and cessation of movement of hyenas are closely associated with sunrise and sunset and the majority of daytime movement occurred in the early morning (Kolowski et al., 2007). Male hyenas tended to exhibit higher movement rates than females over a 24-h period (Kolowski et al., 2007). Movement rates of males peaked at 00:00–01:00 h, but movements of females did not show a clear peak (Kolowski et al., 2007). The maximum distance moved in a single hour was 4,680 m by a male hyena and 4,513 m by a female (Kolowski et al., 2007). Various studies indicated seasonal variation in movements of hyenas due to fluctuations in prey abundance (Hofer & East, 1993; Trinkel et al., 2004).

1.2.3 Sex and social organization

The secondary reproductive organs of hyena are very similar in males and females (Mills & Hofer, 1998). The female clitoris is very similar in size and shape to the male penis. It can be erected and it is situated in exactly the same position as the penis in a male hyena (Mills & Hofer, 1998). Differentiating male and female hyenas by observation in a field is quite problematic. Teats or udders may be visible anterior to the hind legs of an adult female, and the adult female often has ‘baggy’ appearance whereas males are generally quite leggy and trim (Mills & Hofer, 1998). Unlike with most mammals, adult female hyenas are roughly 10% larger than adult males, and are more aggressive and socially dominant (Smith & Holekamp, 2010). Male hyenas disperse after puberty whereas female hyenas generally spend their entire lives in their natal clans (Henschel & Skinner, 1987; Smale et al., 1997; Holekamp & Smale, 1998). Males that successfully immigrate are subordinate to all natal females and their offspring in the new clan (Tilson & Hamilton, 1984; Smale et al., 1993).

Hyenas live in social groups called clans (Kruuk, 1972; Holekamp et al., 1997, 2000) containing 6–90 individuals (Smith & Holekamp, 2010). The mean clan size across Africa is approximately 21 hyenas, but abundance of local prey animals determines clan size (Smith & Holekamp, 2010). Within the territory defended by each clan, individuals travel, rest, and forage alone or in subgroups (Holekamp et al., 2000). Composition of subgroups typically changes several times during the course of a single day and sizes of subgroups range from one to tens of animals (Holekamp et al., 1997, 2000). Hyenas assemble for reasons ranging from such cooperative activities as territorial defense (Henschel & Skinner, 1991; Boydston et al., 2001) to intense direct competition during group feeding at kills of ungulates (Tilson & Hamilton, 1984; Frank, 1986). Hyenas also frequently congregate at the communal den, which serves as the clan’s social center (Boydston et al., 2003). Females with young cubs visit the den regularly to nurse their dependent offspring, and sub-adults, adult males, and adult females without den-dwelling cubs also visit the communal den frequently (Boydston et al., 2003).

1.2.4 Hyena-human interrelation

Conflicts between predators and humans have intensified across Africa due to human population growth and economic activities (Woodroffe, 2000; Conover, 2002). Human–hyena conflict is a common problem on the Afri-

can continent (Ogada et al., 2003; Patterson et al., 2004; Kolowski & Holekamp, 2006; Holmern et al., 2007). Conflict between predators and humans is the main threat to the survival of carnivore species, including hyenas (Woodroffe & Ginsberg, 1998), but this problem is worse in other countries of Africa than Ethiopia. In Ethiopia, depredation of livestock by hyenas appears to be tolerable and is relatively low compared to reports on livestock depredation across Africa (Abay et al., 2011; Yirga et al., 2012b).

A large number of studies reported serious conflicts between hyenas and humans in Africa, resulting in persecution of the hyenas. In the Maasai steppe, Tanzania, the impact of livestock depredation by hyenas was high enough to provoke pastoralists into retaliating against hyenas (Kissui, 2008). Hyenas were the most frequent predators on livestock, followed by lions and leopards and as a result 71 hyenas were reported to have been poisoned in three villages (Kissui, 2008).

Persecution has led to the decline of many populations of large carnivores outside protected areas (Gittleman et al., 2001; Woodroffe, 2001). Studying human-carnivore conflict, including attitudes and actions of local communities toward large carnivores, is very important for the conservation of large carnivores outside protected areas (Sillero-Zubiri & Laurenson, 2001; Naughton-Treves et al., 2003).

Even though hyenas are regarded in a generally negative light in most African cultures, being seen as selfish, foolish, sly, immoral, and dirty (Jürgen, 1998; Glickman, 1995; Middleton & Winter, 2004), they have a positive reputation in some parts of Africa. For example, in the East African Tabwa mythology, hyenas represent the animal that first brought the sun to warm the cold earth (Jürgen, 1998). In Tanzania, killing a hyena in retaliation of an attack is believed to be dangerous because the bond between the hyena and its 'owner' is strong and could result in death of the hyena's killer (Middleton & Winter, 2004). This demonstrates that people across the African continent have different beliefs and practices in relation to hyenas.

The hyena has been hunted for the use of its body parts in traditional medicine (Glickman, 1995; Mills & Hofer, 1998). In the African continent, the hyena body parts are used for medicinal and magical purposes. For example, In Burkina Faso, the hyena's tail, in Cameroon, Côte d'Ivoire and Senegal, the hyena's whole body, in Malawi and Tanzania, the genitalia, nose tips and tails, and in Mozambique the hyena paws are used for traditional medi-

cine (Mills & Hofer, 1998). Hyena's bone is used traditionally for Bouda (evil eye) treatment in Ethiopia.

1.3 Research aims

This study focused on hyena, which is the largest predator in Tigray regional state of Ethiopia. Anthropogenic food sources are of major importance for the survival of hyenas, because natural prey biomass is highly depleted. Overall, this research project aimed to investigate hyena ecology and behavior in human-dominated areas in the Tigray region. This included studies on abundance and distribution, diet, economic impact, human perception, and adaptability of spotted hyenas to changing anthropogenic food sources. The Ethiopian Orthodox Tewahedo Church has unique rules and guidelines for fasting. There are seven fasting periods in a year and all fasts are mandatory for all members of the church. The longest fasting period is the Great Fast (Lent) which is a 55-day fast before Easter. The majority of people in the region do not eat meat and dairy products during this period.

Based on regular observations of hyenas and anecdotal reports, I hypothesized that hyenas in Tigray survive in human-dominated landscapes because of a unique combination of adaptation to anthropogenic food and cultural tolerance towards hyenas.

The specific research questions were:

- 1 What does hyena diet in Tigray consist of and how does it vary in space and time?
 - a What are the changes in diet before, during and after the Orthodox fasting periods?
 - b What are the differences in diet between inside and outside protected areas?
- 2 To what extent are hyenas tolerated by local communities?
- 3 Which factors influence the abundance, density and distribution of hyenas?
 - a What is the abundance and density in prey-depleted areas?
 - b What is the influence of human settlement?
- 4 What is the level of livestock depredation by hyena compared to leopard and jackal in time and space?
 - a Which livestock species are preferred?
 - b What is the trend of livestock depredation?

1.4 Study area

1.4.1 Ethiopia

Ethiopia is the third populous country in Africa with about 85 million people with in an area of 1.1 million square kilometers. The weather is usually sunny and dry with the short ('belg') rains occurring from February to April and the big ('meher') rains beginning in mid-June and ending in mid-September. The livestock population of Ethiopia is among the largest in the world and the largest in Africa, totaling up to 134 million (NABC, Netherlands- African Business Council, 2010).

1.4.2 Tigray regional state

Tigray National Regional State (hereafter Tigray), established in 1993 as one of the nine regional states of Ethiopia, is located in the northeastern part of the country and covers an area of approximately 53,000 square kilometers (Solomon, 2005 cited in Sara, 2010). Administratively, it is divided into six zones, 34 rural districts and 12 town districts (Fig. 1). Each district is subdivided into sub-district (*tabias*) and each tabia is divided into kushet (*hamlets*) which are the lowest unit in the administrative hierarchy. The delineation is made based on natural boundaries such as rivers, escarpments and mountain peaks, population size, agro-ecology and proximity to administrative centers (Sara, 2010). Annual mean temperatures of the region range from 12 °C in some highland areas to 37 °C in Humera (lowland area). The annual mean temperature for most of the region is between 15-21 °C (Sara, 2010). Severe droughts have affected the region every 2-3 years. The region belongs to the African dry lands, which is often called the Sudano-Sahelian region (Warren & Khogali, 1992).

According to Sara (2010) average annual rainfall varies from about 200 mm in the northeastern lowlands to over 1000 mm in the southwestern highlands. The major types of land cover are bush and shrubland (36.2%), cultivated land (28.2%) and grassland (22.8%). Other forms of land cover account for about 11% of the land mass. Cultivated land is the dominant land use in the highlands of Tigray, where there is high human population density (Sara, 2010). Tigray has approximately 4.3 million inhabitants, most of them (81.2%) living in rural areas, with an average family size of five persons per household (Central Statistical Agency, 2008). The population is growing at 2.5% per year and population density in the region is 63 persons per square km (Central Statistical Agency, 2008). Other studies, however, have

indicated that in the highland areas the average density is 137 persons per square km, indicating that there is high population pressure in these areas (Pander & Gebremedehin, 2004). Agriculture is the mainstay of the region's economy, contributing about 57% of the gross domestic product (GDP), of which 36% is from crops, and about 1 and 4% from livestock and forestry, respectively. Forests have been completely converted into farms and grazing lands throughout the region over centuries, except for patchy remnants of old-growth Afromontane forests around most of the old Ethiopian Orthodox Tewahido Churches (Aerts et al., 2007; Alemayehu., 2007). In this study, Wukro and Enderta districts were selected, as they are very near to Mekelle, the regional capital.

1.4.3 Enderta district

Enderta district is one of the eight districts of the southern zone of Tigray (Fig. 1). Mekelle is located in the middle of Enderta district. The district is geographically located between 13°-14° North and at 39°-40° 30' East (Sara, 2010). The total rural human and livestock population is about 115,000 and 56,000, respectively (Bureau of Agricultural and Natural Resources Development (BOANR), 2009). Average family size is five and population density of the district is 79 persons per square km (Sara, 2010). The altitude of the district ranges from below 1400 m a.s.l. to 2700 m a.s.l. The rainfall of the area is bimodal with a short rainy season occurring between January and April, and a long rainy season from June to August. The average annual rainfall of the district is about 550 mm. The mean maximum temperature ranges between 12 °C (November and December) and 27 °C (January and March).

There are 17 *tabias* in Enderta district: Dergi-Ajen, Meseret, Lemlem, May-Genet, Didba, May-Tsedo, Shibta, Felege-Selem, Arato, May-Alem, May-Anbesa, Debri, Mehabere- Genet, Mesebo, Felege-Mayat, Maryam-Liham and Chelekot (Teferi et al., 2011). Landscape formation of the district varies from mountainous, undulating, rugged valleys and gorges, and hilly areas to flat plains (Sara, 2010). The land is severely eroded as a result of continuous human land exploitation and deforestation and natural calamities such as drought. The district has a total area of 193,309 ha, of which the total area of agriculture covers about 49.03%. The average land holding per household is 0.75 ha (Sara, 2010). More than 80% of the population living in the district is engaged in subsistence farming, with land size of less than one ha. The agricultural fields are fragmented over a wide range of different landforms. There are a few established 'enclosures' in the district, mainly for environmental rehabilitation of sensitive areas.

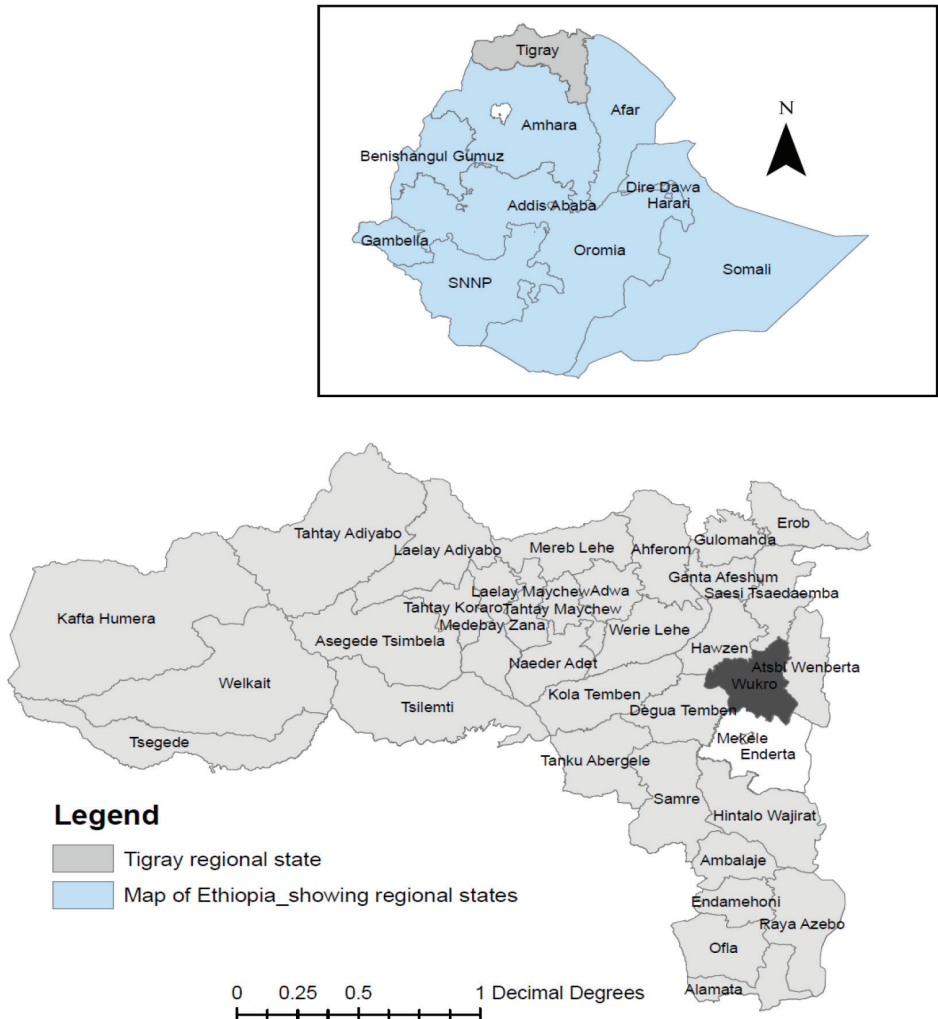


Figure 1.1
 Map of Ethiopia showing regional states and map of Tigray regional state showing Wukro and Enderta districts

1.4.4 Wukro district

The Wukro district is found in eastern zone of Tigray region located at 13° 36' North and 39° 36' East at an altitude of 1,800 to 3,069 m a.s.l (Sara, 2010). The annual temperature and rainfall of the district ranges from 17.25 to 28 °C, and 350 to 450 mm, respectively. The rainfall of the area is bimodal with a short rainy season occurring between January and April, and a long rainy season from June to August. The district has a population of 112,235

persons, giving a human population density of 98 persons per square km (Office of Agriculture and Rural Development of Wukro district, 2010). Average family size is five persons. About 95% of the population of the district depends on rain-fed agriculture and practice livestock husbandry and crop production simultaneously. The average land holding per household is about 0.5 ha. According to Sara (2010) the main crops grown in the district are barley, wheat, teff, maize and sorghum. The livestock population of the district is 209,024 (Sara, 2010). The district has a total area of 100,228 ha. Food insecurity and poverty are severe. The area is generally a seriously degraded landscape with some acacia (*Acacia etbaica*, *Acacia saligna* and *Dodonaea angustifolia*), eucalyptus (*Eucalyptus camaldulensis* and *Eucalyptus globulus*) and African olive (*Olea africana*) vegetation and few large or medium-sized natural prey. There are a few established 'exclosures' in the district; these are very small protected areas mainly for environmental rehabilitation of sensitive areas.

1.5 Outline of the thesis

The first part of the thesis is a general introduction and review of the ecology of hyena and presents the objectives of the study. The country and the area where the study took place are described.

The second part describes the ecology of the spotted hyena:

- In chapter 2, the ecology of peri-urban hyenas in northern Ethiopia is presented. This examines spotted hyena abundance and contribution of livestock depredation and scavenging to hyena food intake.
- Chapter 3 reports on the adaptability of large carnivores to changing anthropogenic food sources. In this chapter, diet change of hyenas during Christian fasting periods is investigated.
- Chapter 4 reports the coexistence of hyena at high density with people in a degraded and prey-depleted district.
- In chapter 5, ecological factors influencing hyena abundance and distribution in anthropogenic landscapes are identified.
- Chapter 6 is about hyena dependence on anthropogenic food across Ethiopia. This chapter presents the diet of spotted hyena based on scat analysis in protected and non-protected areas across Ethiopia.
- Chapter 7 presents the ecology of large carnivores in the highlands of northern Ethiopia. This chapter reports prey preferences of three large carnivores with regard to livestock, and depredation in time and space.

The third part of the thesis (Chapter 8) discusses the implications of the study and mentions some aspects that remain to be better studied.

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