

Ecology and conservation of spotted hyena (Crocuta crocuta Erxleben 1777)in human dominated landscapes in Northern Ethiopia Yirga Abay, G.

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Hyenas (*Crocuta crocuta*) Depend on Anthropogenic Food across Ethiopia

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Abstract

Livestock depredation and scavenging of waste by hyena occurs widely across Ethiopia. Here we report on an extensive survey of depredation in 10 areas across the country. We found that even hyena from national parks predominantly feed on anthropogenic waste. We quantified the economic impact of hyena predation on livestock using semi-structured interviews with 3,080 randomly selected households. They reported losses of 2,230 domestic animals, 3.9% of their stock or an average annual financial loss of US \$10.3 per household, over the past five years. The diet of hyenas was assessed in 17 areas across the country, including national parks, by scat analysis and showed only prey items of domestic origin except in Chebera Churchura national park where a few items of prey of wild species were found. Frequencies of prey remains of cattle, sheep, donkey, and goat were highest in decreasing order. Some hairs in scat originated from depredation, but most food intake was from waste dumps and slaughterhouses. Survival of hyenas in Ethiopia is thus largely and widely dependent on management of livestock conflict and waste. Further research should identify the specific causes of domestic animal loss and options to mitigate depredation.

6.1 Introduction

Large carnivores need areas so vast that they usually include human-dominated landscapes, leading to conflict. Human-carnivore conflict in terms of livestock depredation and human attack is common across the world. Examples include the lynx (Lynx pardinus) (Odden et al., 2002), puma (Puma concolor) and jaguar (Panthera onca) (Conforti & Azevedo, 2003; Zimmermann et al., 2005), lion (Panthera leo) (Ogada et al., 2003; Patterson et al., 2004; Bauer et al., 2010; Sogbohossou et al., 2011), tigers (Panthera tigris) (Wang & Macdonald, 2006), wild dogs (Lycaon pictus) and hyenas (Kolowski & Holekamp, 2006; Yirga & Bauer, 2010; Abay et al., 2011). Across species, predator home range size is related to metabolic energy requirements based on body mass (Gittleman & Harvey, 1982) and loss of resources to intraspecific competitors (Jetz et al., 2004). For example, servals (Leptailures serval) have an average home range of 1.5 km², leopards (Panthera pardus) 23.6 km², and lions 240.0 km² (Gittleman & Harvey, 1982). Hyenas have a lower critical reserve size (179 km²) than expected for a social carnivore that runs down its prey, but this may be due to scavenging and kleptoparasitism (Mills, 1990). This combination of hunting, passive scavenging, and power scavenging (kleptoparasitism), may allow for greater resource utilization over a smaller range (Mills, 1990).

The diet of hyenas has received considerable attention in the scientific literature (Kruuk, 1972; Bearder, 1977; Mills, 1990; Yirga et al., 2012). Hyenas are opportunistic feeders and do not have distinct prey species preference (Hayward, 2006). They are highly adaptive feeders; they are hunters of large or medium prey and scavengers of human waste, bones, dung and even anthrax-infested carcasses (Yirga et al., 2012). They are able to quickly adapt to seasonal fluctuations of prey abundance (Kruuk, 1972; Holekamp et al., 1997; Cooper et al., 1999). In many parts of their range, spotted hyenas have adapted well to dense human populations (Mills & Hofer, 1998; Woodroffe, 2001; Yirga et al., 2012). They primarily feed on wild prey in East Africa but have long been known to depend more on anthropogenic food sources in the Horn of Africa (Gade, 2006). In northern Ethiopia, due to the lack of wild prey, hyenas depend entirely on domestic prey species, partly through depredation but more importantly through scavenging on (peri-) urban waste (Abay et al., 2011; Yirga et al., 2012). Cultural-religious conditions allow coexistence between hyenas and humans in Ethiopia. The present study was initiated to investigate the diet of spotted hyenas in protected and non-protected areas in Ethiopia.

6.2 Study area

Ethiopia is the second populous landlocked country located in the horn of Africa with a total area of 1.1. million km² Our research focused on five regional states (17 sub-districts, Oromia (4), Tigray (9), Afra (2), Amhara (1) and Southern Nation Nationalities Peoples Regional State (1)) of Ethiopia (Fig. 6.1). The sub-districts are located in similar ecological regions (>2000 m a.s.l.) except the Afar region which is a low land area (Fig. 6.1).

6.3 Methods

6.3.1 Semi-structured interviews

We interviewed 3,080 randomly selected heads of households from 10 sub-districts in four regional states of Ethiopia from October, 2009 through April, 2010. Households were selected assigning numbers and using a rand-omized table per study area. Respondents were asked questions relating to

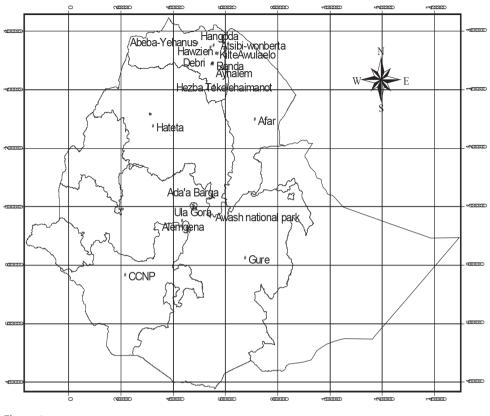


Figure 1 Location of 17 sites across five regional states of Ethiopia

number of domestic animals owned, management and number of domestic animals lost to hyena predation from 2006-2010, the period for which depredation was recorded. To quantify the economic cost of livestock depredation, the species, age, number, and sex of domestic animals lost were recorded. Estimates of current average market prices of different classes of domestic animals by age and sex were obtained from traders. Prices were translated to US\$ at the exchange rate of the time of the study (March-May, 2010). The reported predation events or financial costs may not be entirely accurate, as depredation counts are based on reports by farmers. However, there have never been any incentives (monetary compensation for livestock depredation) in the study area for interviewees to exaggerate depredation claims. We established a correlation between livestock abundance and reported depredations obtained from interviews. All statistical tests and correlations were performed using JMP-5 Software (Yirga et al., 2012).

6.3.2 Scat analysis

During the study period, a total of 2,006 putative hyena scats were collected from 15 sub-districts in four regional states. Also, scats were collected from Awash and Chebera Churchura national parks, located in Afar and Southern Nation Nationalities Peoples Regional States of Ethiopia, respectively. Hyena droppings were identified using Stuart and Stuart (2000). Scat samples were put in plastic bags with details of collection time, location and characteristics of the substrate from which the scat was collected. Precaution was taken to ensure that there was no cross sample contamination. Scat analysis, which is based mainly on identification of mammalian hairs, is a valuable technique (Mills, 1992), as most prey species can be reliably determined, field collection is rapid, the scats can be stored and processed at a convenient time, and costs are low. Also, usually only one or a few prey species are represented in the scat, which makes determination possible. However, hair frequency does not necessarily correlate with prey volume. The method also does not differentiate between hunting and scavenging.

The procedure described here was adapted from Ramakrishean et al. (1999). After collection of the faeces, the samples were washed with water and hairs were extracted. These hairs were washed in acetone and then dehydrated in ethanol and dried on filter paper. Hair was analyzed on the basis of form, length and color with the naked eye as well as on scale patterns using a microscope at 10x magnification. The hairs were compared with our hair reference collection. This reference hair collection contained hairs from all domestic and wild animal species that live in and around the study area.

Jacobs' indices were calculated to determine preference for each domestic prey species compared to availability. Data obtained from interviews was used as the measure of prey abundance and reported depredations were used as the measure of prey selection. To identify the preferable species of livestock, Jacobs' index was calculated using the formula

$$D = \frac{r - p}{r + p - 2rp}$$

where r is the proportion of the total kills at site made up by a species and p is the proportional availability of the prey species, the resulting value ranges from +1 to -1, where +1 indicates maximum preference and -1 indicates maximum avoidance (Jacobs, 1974).

6.4 Results

6.4.1 Prey preference

The diet of hyenas showed only prey items of domestic origin except in Chebera Churchura national park, where a few wild prey items were found (Table 6.1). Frequencies of prey remains of cattle, sheep, donkey and goat were highest, in decreasing order. Table 6.3 presents Jacobs' index scores derived from 2,030 reported losses of 12 domestic prey species.

Table 6.1

Frequency of occurrence of hair from prey species in hyena scat (n = 2,006) in five regional states of Ethiopia

| Species | Oromia | Tigray | Afar | SNNPRS | Amhara | Total | Relative frequency (%) |
|------------------|--------|--------|------|--------|--------|-------|---------------------------|
| Donkeys | 21 | 252 | 9 | 0 | 3 | 285 | 14.2 |
| Sheep | 8 | 301 | 4 | 8 | 3 | 324 | 16.2 |
| Goats | 6 | 161 | 14 | 7 | 8 | 196 | 9.8 |
| Cattle | 50 | 317 | 24 | 19 | 10 | 420 | 20.9 |
| Camel | 0 | 26 | 6 | 0 | 0 | 32 | 1.6 |
| Human | 1 | 102 | 0 | 0 | 0 | 103 | 5.1 |
| Mules | 8 | 86 | 0 | 0 | 6 | 100 | 5 |
| Poultry | 0 | 24 | 0 | 0 | 0 | 24 | 1.2 |
| Dog | 0 | 127 | 0 | 0 | 0 | 127 | 6.3 |
| Cat | 0 | 9 | 0 | 0 | 0 | 9 | 0.5 |
| Porcupine | 0 | 1 | 0 | 0 | 0 | 1 | 0.05 |
| Hare | 0 | 1 | 0 | 0 | 0 | 1 | 0.05 |
| Horse | 2 | 239 | 0 | 0 | 0 | 241 | 12 |
| Waterbuck | 0 | 0 | 0 | 8 | 0 | 8 | 0.4 |
| Bushbuck | 0 | 0 | 0 | 7 | 0 | 7 | 0.3 |
| Kudu | 0 | 0 | 0 | 6 | 0 | 6 | 0.3 |
| Common duiker | 0 | 0 | 0 | 3 | 0 | 3 | 0.2 |
| Unidentified | 2 | 82 | 7 | 2 | 0 | 93 | 4.6 |
| Hairless samples | 0 | 26 | 0 | 0 | 0 | 26 | 1.3 |
| Total | 98 | 1754 | 64 | 60 | 30 | 2006 | 100 |

*The reference hair collection also included natural prey species, but these did not match the unidentified hairs. The wild prey waterbuck, bushbuck, kudu and common duiker were from CCNP. SNNPRS-Southern Nation Nationalities Peoples Regional State.

Table 6.2

Stock quantities, depredation and economic impact of hyenas from 2006-2010 in 10 sub districts in four regional states of Ethiopia, Oromia (number of respondents, n = 1,400), Tigray (n = 1,330), Afar (n = 150) and Amhara (n = 200)

| | | Stock | ck k | | Ō | Depredation (% of stock) | % of stock) | | | Economic | Economic loss (US\$) | |
|---------|--------|--------|---------|--------|------------|--------------------------|-------------|-----------|--------|----------|----------------------|--------|
| Species | Oromia | Tigray | Afar | Amhara | Oromia | Tigray | Afar | Amhara | Oromia | Tigray | Afar | Amhara |
| Donkeys | 1710 | 785 | 63 | 0 | 152(8.9) | 113(14.4) | 5(7.9) | 0(0) | 10640 | 7910 | 350 | 0 |
| Sheep | 7617 | 4835 | 1836 | 1339 | 382(5) | 140(2.9) | 116(6.3) | 170(12.7) | 6112 | 2800 | 2088 | 3400 |
| Goats | 2617 | 2028 | 2115 | 0 | 133(5.1) | 41(2.02) | 129(6.1) | 0(0) | 1995 | 652 | 2064 | 0 |
| Cows | 5102 | 2131 | 1543 | 617 | 78(1.5) | 20(0.9) | 90(5.8) | 19(3.1) | 11700 | 3300 | 14400 | 3040 |
| Poultry | 4843 | 3369 | 0 | 849 | 23(0.5) | 7(0.2) | 0(0) | 0(0) | 57 | 18 | 0 | 0 |
| Dogs | 1577 | 844 | 123 | 75 | 113(7.2) | 39(4.6) | 6(4.9) | 12(16) | 226 | 78 | 12 | 28 |
| Bulls | 923 | 1197 | 447 | 12 | 16(1.7) | 24(2) | 45(10.1) | 0(0) | 5120 | 7680 | 14400 | 0 |
| Oxen | 3363 | 1511 | 344 | 231 | 70(2.1) | 13(0.9) | 25(7.3) | 2(0.9) | 14000 | 2600 | 5000 | 400 |
| Calves | 631 | 423 | 65 | 188 | 12(1.9) | 25(5.9) | 15(23.1) | 43(22.9) | 768 | 1700 | 1020 | 2752 |
| Mules | 46 | 12 | 0 | 13 | 18(39.1) | 0(0) | 0(0) | 3(23.1) | 2592 | 0 | 0 | 432 |
| Horses | 861 | 29 | 0 | 367 | 45(5.2) | 1(3.5) | 0(0) | 78(21.3) | 7560 | 168 | 0 | 13104 |
| Camels | 0 | 14 | 250 | 0 | 0(0) | 0(0) | 19(7.6) | 0(0) | 0 | 0 | 7308 | 0 |
| Total | 29,290 | 17,178 | 6,786 | 3,691 | 1,030(3.5) | 423(2.5) | 450(6.6) | 327(8.9) | 60,770 | 26,906 | 46,642 | 23,156 |

6.4.2 Depredation of domestic animals

Respondents indicated a total loss of 2,230 domestic animals to hyena predation, or 3.9% of their stock, over the past five years. This predation represented an estimated financial loss of US\$ 157,474 over five years, or an annual mean damage US\$ 31,497 (Table 6.2). The costs due to domestic animal loss were on average US \$10.30 per household.

Table 6.3

Prey preference of hyena based on analysis of 2,030 depredated livestock from 3,080 respondents in four regional states of Ethiopia over the last five years

| | | Jacobs in | dex value | |
|---------|--------|-----------|-----------|--------|
| Species | Oromia | Tigray | Afar | Amhara |
| Donkeys | 0.47 | 0.77 | 0.1 | 0 |
| Sheep | 0.25 | 0.12 | -0.03 | 0.31 |
| Goats | 0.2 | -0.11 | -0.06 | 0 |
| Cows | -0.44 | -0.48 | -0.08 | -0.53 |
| Poultry | -0.79 | -0.87 | 0 | 0 |
| Dogs | 0.37 | 0.33 | -0.16 | 0.29 |
| Bulls | -0.33 | -0.11 | 0.22 | 0 |
| Oxen | -0.28 | -0.5 | 0.05 | -0.83 |
| Calves | -0.3 | 0.43 | 0.56 | 0.48 |
| Mules | 0.84 | 0 | 0 | 0.45 |
| Horses | 0.21 | 0.17 | 0 | 0.48 |
| Camels | 0 | 0 | 0.07 | 0 |

6.5 Discussion

The majority of prey items found in the scat analyses came from livestock species. It is likely that most of the human hairs found (n=103) came from scavenging at garbage dumps and cemeteries, as we do not have reports of people killed by hyenas at the time of study. Even within the two national parks, Awash and Chebera Churchura, prey remains of domestic species were dominant. This presents a new finding on hyena diets in national parks, as previous studies showed a variety of prey, predominantly wild prey (Honer et al., 2002; Hayward, 2006; Trinkel, 2010). This is probably due to very low densities of natural prey in these national parks, and/or due

to scavenging around the houses of park rangers and near villages. There is also extensive illegal grazing and livestock encroachment in these parks, as is evident in almost all Ethiopian national parks.

We have shown how important domestic animals are in the diet of hyenas. We postulate that depletion of natural prey species forces hyena to depend on anthropogenic food sources, which is why hyenas commonly occur in suburban and urban areas across Ethiopia. Carnivore densities in natural ecosystems generally reflect the abundance of their prey (Bertram, 1975; Fuller & Sievert, 2001). A positive correlation exists between carnivore density and natural prey abundance in many ecosystems of the world (Karanth et al., 2004; Hetherington & Gorman , 2007; Croes et al., 2011).

Hyenas have adapted to human-dominated habitats across Ethiopia and benefit from waste disposal. Cultural-religious practices allow coexistence between hyenas and humans. Scavengers such as raccoons (Procyon lotor), opossums (Didelphis virginiana), crows (Corvus spp.), and gulls (Larus spp.) and some opportunistic generalist carnivores such as foxes (Vulpes spp.) and covotes (*Canis latrans*) are increasingly common in urban habitats, suggesting that the relatively high abundance of food attracts wildlife to urban areas (Adams et al., 2006; Sauter et al., 2006). Urban ecosystems are typically characterized by increased abundance of a few species able to exploit anthropogenic food sources (Newsome et al., 2010). In our case, hyena is increasingly common in suburban and urban habitats, as it is attracted by garbage left in the streets and open areas. In many towns in Ethiopia such as Addis Ababa, Gondar, Jijiga and Mekelle, hyenas have the role of scavenger (Gade, 2006). They have nocturnal access to garbage left in the streets, and are especially attracted to towns with slaughterhouses such as Mekelle (Nikoru, 1972; Henze, 1977). This removal of waste of butchers and households near towns or cities contributes substantially to their persistence in dense human populations.

Hyenas are common across Ethiopia, and in most of those areas prey populations appear small (Abay et al., 2011). Hyenas are highly adaptable and opportunistic hunters and scavengers (Yirga et al., 2012). Their nocturnal and opportunistic foraging behavior, together with the ability of hyenas to take long-distance commuting trips, makes them particularly adaptable to anthropogenic environments (Kruuk, 1972; Hofer & East, 1995; Mills & Hofer, 1998). In the present study, frequencies of prey remains of cattle, sheep, donkey and goat were highest, in decreasing order. Unlike other large carnivores, hyenas do not exhibit a preference for any species of prey (Hayward, 2006). The lack of prey preferences might be due to the fact that they are able to meet their food requirements through scavenging (Hayward, 2006). Hyenas in Ethiopia have mostly lived in anthropogenic context rather than, as in East Africa, on wildlife (Gade, 2006).

Quantifying hyena predations on livestock might be important to mitigate the effects and to promote a more stable coexistence of hyenas and humans. More detailed information on the intensity of predation on livestock is important for developing strategies for conserving carnivores (Polisar et al., 2003). Herd management has been identified as a factor in predation rate (Patterson et al., 2004; Frank et al., 2005). More thoughtful and informed herd management has the potential to reduce losses (Rasmussen, 1999). Conservation efforts can be improved by raising the tolerance of pastoralists for wild carnivores through educational and economic incentives (Marker et al., 2003). Ogada et al. (2003) found improved enclosures to be effective against large carnivores.

In this study, 170 dogs were declared victims of hyena predation. Most likely, this is an underestimate of the numbers of field or stray dogs preyed upon. About 70% of dogs have no owners and would not be reported in depredation surveys. It is clear that in this case, hyena actively chased and killed domestic dogs. Various researchers have reported that dogs do not reduce nocturnal livestock predation by hyenas and lions (Kolowski & Holekamp, 2006; Ikanda & Packer, 2008), but Woodroffe et al. (2007) reported that dogs improved livestock security both in the daytime grazing fields and in the bomas at night. Since their early domestication, dogs have acted as an early warning system for approaching predators and visitors to human settlements (Coppinger & Coppinger, 2001). In our study, domestic dogs were clearly ineffective in protecting villages from hyena attacks.

Our study has shown that scavenging of waste and livestock depredation by hyenas occurs widely across Ethiopia. Hyenas in Ethiopia predominantly depend on anthropogenic food sources rather than natural prey. Survival of hyenas is largely and widely dependent on management of livestock conflict and waste disposal.

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References

- Abay, G.Y., Bauer, H., Gebrihiwot, K. & Deckers, J. (2011). Peri-urban spotted hyena (*Crocuta crocuta*) in northern Ethiopia: diet, economic impact, and abundance. European Journal of Wildlife Research 57, 759-765.
- Adams, C.E., Lindsey, K.J. & Ash, S.J. (2006). Urban Wildlife Management. CRC Press, Boca Raton, FL.
- Bauer, H., De Iongh, H.H. & Sogbohossou, E. (2010). Assessment and mitigation of human-lion conflict in West and central Africa. Mammalia **74**, 363-367.
- Bearder, S.K. (1977). Feeding habits of spotted hyenas in woodland habitat. East African Wildlife Journal 14, 233-235.
- Bertram, B.C.B. (1975). Social factors influencing reproduction in wild lions. Journal of Zoology (London) 177, 463-482.
- Conforti, V.A. & Azevedo, C.C. (2003). Local perceptions of jaguars (*Panthera onca*) and pumas (*Puma concolor*) in the Iguacu National Park area, south Brazil. Biological Conservation **111**, 215-221.
- Cooper, S.M., Holecamp, K.E. & Smale, L. (1999). A seasonal feast: long-term analysis of feeding behavior in the spotted hyena (*Crocuta crocuta*). African Journal of Ecology **37**, 149-160.
- Coppinger, R. & Coppinger, L. (2001). Dogs: A Startling New Understanding of Canine Origin, Behavior, and Evolution. Scribner, New York.
- Croes, B.M., Funston, P.J., Rasmussen, G., Buij, R., Saleh, A., Tumenta, P.N. & De Iongh, H.H. (2011). The impact of trophy hunting on lions (*Panthera leo*) and other large carnivores in the Bénoué Complex, northern Cameroon. Biological Conservation 144, 3064-3072.
- Frank, L.G., Woodroffe, R. & Ogada, M.O. (2005). People and predators in Laikipia District, Kenya. In: Woodroffe, R., Thirgood, S. & Rabinowitz, A. eds. People and Wildlife: Conflict or Coexistence (pp. 286-304)? Cambridge University Press: Cambridge, United Kingdom.

- Fuller, T.K. & Sievert, P.R. (2001). Carnivore demography and the consequences of changes in prey availability. In: Gittleman, J.L., Funk, S.M., Macdonald, D.W. & Wayne, R.K. eds. Carnivore Conservation (pp. 163-178). Cambridge University Press and the Zoological Society of London: Cambridge, United Kingdom.
- Gade, D.W. (2006). Hyenas and humans in the Horn of Africa. Geographical Review **96**, 609-632.
- Gittleman, J.L. & Harvey, P.H. (1982). Carnivore home-range size, metabolic needs and ecology. Behavioral Ecology and Sociobiology **10**, 57-63.
- Hayward, M.W. (2006). Prey preferences of the spotted hyena *Crocuta crocuta* and evidence of dietary competition with lion *Panthera leo*. Journal of Zoology (London) **270**, 606-614.
- Henze, P.B. (1977). Ethiopian Journeys: Travels in Ethiopia 1969-72. London: Ernest Benn.
- Hetherington, D.A. & Gorman, M.L. (2007). Using prey densities to estimate the potential size of reintroduced populations of *Eurasian lynx*. Biological Conservation 137, 37-44.
- Hofer, H. & East, M.L. (1995). Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. In: Sinclair, A.R.E. & Arcese, P. eds. Serengeti II: Dynamics, Conservation, and Management of an Ecosystem (pp. 332–363). University of Chicago Press: Chicago, USA.
- Holekamp, K.E., Smale, L., Berg, R. & Cooper, S.M. (1997). Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). Journal of Zoology (London) 242, 1-15.
- Höner, O.P., Wachter, B., East, M.L. & Hofer, H. (2002). The response of spotted hyenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. Journal of Animal Ecology 71, 236-246.
- Ikanda, D.K. & Packer, C.C. (2008). Ritual vs. retaliatory killing of African lions in the Ngorongoro Conservation Area. Tanzania. Endangered Species Research 6, 67-74.
- Jacobs, J. (1974). Quantitative measurement of food selection a modification of the forage ratio and Ivlev's electivity index. Oecologia **14**, 413-417.
- Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. (2004). The scaling of animal space use. Science, **306**, 266-268.
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A. & Hines, J.E. (2004). Tigers and their prey: predicting carnivore densities from prey abundance. Proceedings of the National Academy of Science USA 101, 4854-4858.
- Kolowski, J.M. & Holekamp, K.E. (2006). Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. Biological Conservation **128**, 529-541.
- Kruuk, H. (1972). The Spotted Hyena: a Study of Predation and Social Behavior. University of Chicago Press: Chicago.

- Marker, L.L., Mills, M.G.L. & Macdonald, D.W. (2003). Factors influencing perceptions of conflict and tolerance toward cheetahs on Namibian farmlands. Conservation Biology 17, 1290-1298.
- Mills, G. & Hofer, H. (1998). Hyenas: Status Survey and Conservation Action Plan. World Conservation Union, Gland, Switzerland.
- Mills, G.G.L. (1990). Kalahari hyenas: comparative behavioral ecology of two species. London. Unwin Hyemn.
- Mills, M.G.L. (1992). A comparison of methods used to study food habits of large African carnivores. In: McCulloch, C. & Barret, R.H. eds. Wildlife 2001: Populations (pp. 1112-1123). Elsevier: London.
- Newsome, S.D., Ralls, K., Job, C.V., Fogel, M.L. & Cypher, B.L. (2010). Stable isotopes evaluate exploitation of anthropogenic foods by the endangered San Joaquin kit fox (*Vulpes macrotis mutica*). Journal of Mammalogy **91**, 1313-1321.
- Nikoru, C.W. (1972). From the Roof of Africa. New York: Alfred Knopf
- Odden, J., Linnell, J.D.C., Moa, P.F., Herfindal, I., Kvam, T. & Andersen, R. (2002). Lynx predation on domestic Sheep in Norway. Journal of Wildlife Management **66**, 98-105.
- Ogada, M.O., Woodroffe, R., Oguge, N.O. & Frank, L.G. (2003). Limiting depredation by African carnivores: the role of livestock husbandry. Conservation Biology 17, 1521-1530.
- Patterson, B.D., Kasiki, S.M., Selempo, E. & Kays, R.W. (2004). Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. Biological Conservation 119, 507-516.
- Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M.E. & Eisenberg, J.F. (2003). Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. Biological Conservation **109**, 297-310.
- Ramakrishean, U., Coss, R.G. & Pelkey, N.W. (1999). Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. Biological Conservation 89, 133-120.
- Rasmussen, G.S.A. (1999). Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: a case study. Biological Conservation **88**, 133-139.
- Sauter, A., Bowman, R., Schoech, S.J. & Pasinelli, G. (2006). Does optimal foraging theory explain why suburban Florida scrub-jays (*Aphelocoma coerulescens*) feed their young human-provided food? Behavioral Ecology and Sociobiology 60, 465-474.
- Sogbohossou, E.A., De Iongh, H.H., Sinsin, B., De Snoo, G.R. & Funston, P.J. (2011). Human-carnivore conflicts around Pendjari Biosphere reserve, northern Benin. Oryx 6, 1-10.
- Stuart, C. & Stuart, T. (2000). Tracks and signs of Southern and East African Wildlife. Struik Publishers, Cape Town, pp 310.

- Trinkel, M. (2010). Prey selection and prey preferences of spotted hyenas *Crocuta crocuta* in the Etosha National Park, Namibia. Ecological Research **25**, 413-417.
- Wang, S.W. & Macdonald, D.W. (2006). Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. Biological Conservation 129, 558-565.
- Woodroffe, R. (2001). Strategies for carnivore conservation: lessons from contemporary extinctions. In: Gittleman, J.L., Wayne, R.K., Macdonald, D.W. & Funk, S.M. eds. Carnivore conservation (pp. 61-92). Cambridge University Press: Cambridge, United Kingdom.
- Woodroffe, R., Frank, L.G., Lindsey, P.A., Ole Ranah, S.M.K. & Roman[~] ach, S. (2007). Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case–control study. Biological Conservation 16, 1245-1260.
- Yirga, G., & Bauer, H. (2010). Livestock depredation of the spotted hyena (*Crocuta crocuta*) in Southern Tigray, Northern Ethiopia. International Journal of Ecology and Environmental Sciences **36**, 67-73.
- Yirga, G., De Iongh, H.H., Leirs, H., Gebrehiwot, K., Deckers, J. & Bauer, H. (2012). Adaptability of large carnivores to changing anthropogenic food sources: diet change of spotted hyena (*Crocuta crocuta*) during Christian fasting period in northern Ethiopia. Journal of Animal Ecology 81, 1052-1055.
- Zimmermann, A., Walpole, M. & Leader-Williams, N. (2005). Cattle ranchers' attitudes to conflicts with jaguar *Panthera onca* in the Pantanal of Brazil. Oryx **39**, 406-412.

