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Depredation of Livestock by Wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

Thesis for the degree philosophiae doctor

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PREFACE

This work is an output of the Biodiversity and Human Wildlife Interface (BHWI) in the western Serengeti, a collaborative project between the Tanzania Wildlife Research Institute (TAWIRI), the Norwegian Institute for Nature Research (NINA) and the Norwegian University of Science and Technology (NTNU). The Messerli Foundation of Switzerland, Institute for Zoology and Wildlife Research (IZW) of Germany and the Norwegian Agency for Development Cooperation (NORAD) funded the initial stage of the project between 2001 and 2004. The final stage of this work (2005 and 2007) was financially supported by the Norwegian Peace Corps and the Quota Programme Scheme (NORAD). Among objectives of the BHWI) has been to build research capacity at TAWIRI.

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Table of Contents

THIS THESIS CONSISTS OF THE FOLLOWING FIVE PAPERS.

I Nyahongo, J.W., East, M.L., Mturi, F. & Hofer, H. (2006) Benefits and costs of illegal grazing and illegal hunting in the Serengeti ecosystem. *Environmental Conservation*, 32 (4), 326-332

II Holmern, T., Nyahongo, J. & Røskaft, E. (2007) Livestock loss caused by predators outside the Serengeti National Park, Tanzania. *Biological Conservation*, 135, 534-542.

III Nyahongo, J.W., Holmern, T., Stokke, B.G., Keyyu, J.D., Kaltenborn, B.P. & Røskaft, E. (Submitted) Disease is a mojor cause of livestock loss in villages surrounding western Serengeti, Tanzania.

IV Nyahongo, J.W., Holmern, T., Kaltenborn, B. P. & Røskaft, E. (Submitted) Spatial-temporal variation in meat and fish consumption among humans in the western Serengeti, Tanzania: the importance of migratory herbivores.

V Nyahongo, J.W., Holmern, T., Stokke, B.G., Kaltenborn, B. P. & Røskaft, E. (Submitted) Bushmeat preference and species recognition based on meat taste by humans in the western Serengeti, Tanzania.

Declaration of contribution

EML, MF and HH contributed with ideas, planning for fieldwork, data collection and commenting on paper I. ER contributed with ideas, planning for fieldwork, data collection and commenting on the II, III, IV and V ms throughout. Contribution of the co-authors: Paper II, I provided some data, exchanged some notes, discussed some results and commented on the ms. Paper III, HT, SBG, KJD and KBP commented on the ms. Paper IV, HT and KBP commented on the ms. Paper V, HT, SBG and KBP commented on the ms.

SUMMARY

Human-wildlife interactions play an important role in shaping perceptions and conservation paradigms and the livelihoods in villages neighbouring protected areas. These interactions also determine the future survival of the wildlife in the face of increasing pressure due to high human population increase characterising most countries in sub-Saharan Africa. Most rural people in sub-Saharan Africa are agropastoral, combining small scale farming with animal husbandry, or they are purely agropastoralists or farming who relies on natural resources for sustenance.

The negative impacts from wildlife to humans may include crop damage, attacking and killing livestock and humans, competing for game species or acting as diseases reservoirs. Humans may affect wildlife through a wide range of lethal methods such as shooting, poisoning, trapping or snaring, habitat modification, encroachment or diseases exchange between wildlife and livestock.

Illegal hunting using traditional weapons is wide spread in communities surrounding areas rich of wildlife where in some countries in Africa (i.e. Liberia) up to 75% meat protein is derived from wildlife. The main factors attributing to high consumption of bushmeat is local availability, easy catch-ability (wire snares, pitfall traps), affordability and the consequent household savings.

This thesis evaluates the conflicts between human and wildlife in the human-wildlife interface using the western Serengeti as a case study. The first part of the thesis focuses

on the conflict related to utilization of natural resources and livestock depredation whereas the second part focuses on the dietary contribution of bushmeat to local people, bushmeat experience and utilization.

Local people living close to protected areas are rational when it comes to the illegal utilization of natural resources because they consider the benefits and cost implications. The bushmeat hunters, especially, know in advance which areas in the protected areas are profitable at the same time consider the cost of being arrested and the distance they need to walk to the profitable areas. While illegal hunting can take place far in the park, livestock keepers avoid grazing inside the park because they know the consequences (penalties and fines) of utilizing the pasture inside the protected areas illegally.

The local people living close to protected areas consume more meat meals during the period when the wildebeest are in the village proximities than when the herds are far in the southern plains. This further proves the rationality of illegal bushmeat hunters when planning for hunting trips (the benefits versus cost). In contrast, the fish meals in the villages located close to protected areas but far from Lake Victoria decrease with influx of migratory herbivores, which suggest that fish and meat complement each other when the distance from the sources fluctuates. This was proved true when test-persons from villages close, intermediate and distant from the nearest national park boundary were given pieces of meat in a combination of wild ungulates and beef to rank the meat and species recognition according to the perceived taste. While the test-persons from distant villages preferred beef to all, the test-person from villages close to national park boundary prefer topi and those in the intermediate villages prefer impala. This suggests long term experience with beef to distant test-persons as no other source of meat is locally available in the area other than livestock meat and fish.

Wild carnivores are considered to be responsible for livestock losses in the villages surrounding the protected areas. The results from the current study in the villages surrounding the western Serengeti show that among the wild carnivores reported to kill livestock, 97.7% of all reported claims was spotted hyena, being responsible for 98.2%. Spotted hyenas are nocturnal animals capable of commuting up to 80 km from their territory areas and are the most numerous large carnivore species in the Serengeti ecosystem, mainly targeting goats and sheep. To evaluate the level of conflicts between carnivores and human on livestock depredation, enumeration of livestock loss causes was conducted for subsequent comparison. In all villages, diseases were responsible for major loss of livestock.

Based on the findings the current study recommends better education on wildlife conservation, livestock husbandry practices and extension. A change in wildlife policy in favour of compensation would reduce the retaliatory killing of carnivores in the villages. Livestock keepers should improve the night holding enclosures to reduce livestock depredation by nocturnal predators. The findings recommend further study on the alternative sources of meat protein to local communities living close to protected areas. Last but not least, I recommend a special conservation attention to resident herbivore population close to village proximities.

INTRODUCTION

Human-wildlife interactions play an important role in shaping perceptions and conservation paradigms and the livelihoods in villages neighbouring protected areas. These interactions also determine the future survival of the wildlife in the face of increasing pressure due to high human population increase characterising most countries in sub-Saharan Africa (Ceballos and Ehrlich 2002). Biodiversity is being depleted at a rate that is causing concern among conservation interests worldwide.

The human population in Africa has increased from 224 million in 1950 to 960 million in 2005, and is predicted to reach more than 1.2 billion people by 2030 (UNDP, 2002). Most of this increase will happen in the rural areas, which currently hold 65-85% of the African population (UNDP, 2002). This inevitably will affect the conservation in the future because most rural people in sub-Saharan Africa are agropastoral, combining small scale farming with animal husbandry, or are purely agropastoralists or farming. The future reliance on natural resources (i.e. water, firewood, rangeland for livestock, fish and bushmeat together with mining) for sustenance means exhaustion of their resources base that not only affects conservation and biodiversity but is also a threat to human welfare.

Impact from human-wildlife interactions may be either positive or negative on the parties affected (Conover, 2002). The negative impacts from wildlife to humans may include crop damage (Dey, 1991; Naughton-Treves, 1998), attacking and killing livestock (Mishra, 1997; Ogada et al., 2003), competing for game species (Gasaway et al., 1992; Thirgood et al., 2000) attacking and killing humans (Herero, 1985; Saberwal et al., 1994;

Nowell and Jackson, 1996; Løe and Røskaft, 2004; Packer et al., 2005) or acting as diseases reservoirs (Jenknis et al., 1998; Hudson et al., 2002; Kock, 2003). On the other hand, technological advancements have lead to a wide range of lethal methods for controlling wildlife, such as shooting, poisoning, trapping or snaring (Hofer et al., 1996; Brand and Nel, 1997; Treves and Naughton-Treves, 2005). Indirectly, humans may affect wildlife through habitat modification, encroachment or diseases exchange between wildlife and domestic stock all of which intend to satisfy the humans needs (Kock, 2003).

Carnivore-human conflicts

The common conflicts between humans and wild animals in different parts of the world involve livestock depredation and crop damages. Although a remarkable range of species cause conflicts with humans, from rodents such as prairie dogs (*Cynomys ludovicianus*) to mega-herbivores like African elephants (*Loxodonta africana;*Hoare, 1999), large carnivores are of particular interest in this conflict. This is due to their obligate instinctive carnivorous behaviour, which put them into direct competition with humans for both livestock and wild game species or their ability to kill humans, which create more fear, intensifying the conflicts (Sillero-Zuberi, and Laurenson, 2001; Baldus, 2004; Løe and Røskaft, 2004; Packer, 2005). These perceptions are always compounded by an innate fear of large predators and long term negative attitudes that have developed among humans towards large predators due to the past experiences they had or were told even if carnivores do not pose any threat in present time (Quammen, 2003, Røskaft, 2003; Dickman, 2005). While studies show that large carnivores are not responsible for as much damage as local people commonly perceive (Rasmussen, 1999), this perception of severe conflict is the important factor, as negative attitudes are strongly linked to retaliatory killing of carnivores (Gittleman et al., 2001, Paper II). This has resulted in persecution of wild carnivores in most parts of the world. For instance, angry farmers in Norway were reported to kill wolf (*Canis lupus*) to reduce sheep predation (Kaltenborn *et al.*, 1999), and even today is the conflict between sheep farmers and wolves at a serious level elsewhere several places outside Africa (Røskaft *et al.*, 2003).

Large-scale predator control programs have historically been employed to reduce predator conflicts with humans (Kellert, 1985; Woodroffe, 2000). All predators have suffered persecution with the result that they have been exterminated over most of their former ranges, particularly in Europe, North America and parts of Asia (Ginsberg and Macdonald, 1990; Saberwal *et al*.; 1994; Nowell and Jackson, 1996; Mills and Hofer, 1998). Lethal control of carnivores has resulted in extinction of several species of carnivores. For instance, a combination of trapping for fur and poisons to protect sheep led to the extinction of the Falkland's wolf or Malvinas zorro (*Dusicyon australis*) in 1876 (Sillero-Zubiri et al., 2004). Similarly, conflict with humans was identified as a key factor behind the extinction of the Carolina parakeet (*Conuropsis carolinensis*) in 1904 and that of the thylacine or marsupial wolf (*Thylacinus cynocephalus*) in 1930 (IUCN, 2006; Woodroffe et al., 2005).

In Africa, killing of wild carnivores over livestock depredation has been reported. Berry (1990) reported the killing of at least 320 lions (*Panthera leo*) between 1980 and 1989 on farms bordering the Etosha National Park, Namibia. Stuart *et al.* (1985) reported the killing of leopards (*Panthera pardus*) by farmers due to predation on livestock in the Cape Province, South Africa. Holekamp and Smale (1992) reported that the growing human population around Maasai Mara National Reserves in Kenya poisoned at least 14 spotted hyenas (*Crocuta Crocuta*) in a single incidence in June 1991 to reduce livestock predation.

Even where the carnivore-human conflicts does not result in extinction, it may have a devastating impact on species' population size and geographical range, often leading to local extirpation (Johnson et al., 2001; Treves and Naughton-Treves, 2005). For example, cheetahs (*Acinonyx jubatus*) historically ranged across Africa, Asia and into the Indian sub-continent, with numbers estimated at ca. 100 000 individuals in 1900 (Marker, 1998). However, the population of cheetah has declined to less than 15 000 individuals globally for the past 50 years, and a complete disappearance in at least 13 countries where cheetah has been recorded (Marker, 1998). Similarly, African wild dogs (*Lycaon pictus*) have suffered a severe eradication from 25 of the 39 countries they used to occupy and are now one of the world's most endangered carnivores, with total number estimated to fewer than 5000 individuals, with only six packs thought to hold over 100 individual dogs (Fanshawe et al., 1991; Woodroffe et al., 1997).

The carnivore species causing most conflicts are also those who are most important in ecological maintenance. Large carnivores fulfil many important ecological functions, such as regulating prey numbers (many of them crop pests or water pollutants), controlling number of mesopredators through competition or are maintaining a functional balance of biodiversity in local communities (Krebs et al., 1995; Logan and Sweanor, 2001). Removing top predators from habitat patches often results in marked changes in biodiversity and community structure, which may have severe ecological effects (Terborgh et al., 2002).

Effects of illegal hunting

Illegal hunting using traditional weapons such as snares, bow and arrows is widespread in communities surrounding areas rich of wildlife. Legal hunting on the other hand require the possession of a license and the demand for a license include among others, a fire arm which the majority of people in poor countries rich of biodiversity cannot afford. Illegal hunting is motivated by the need for protein, income and sometimes acts as food especially during prolonged droughts. These and other factors magnify the hunting pressure resulting on the park-people conflicts (Holmern et al., 2004).

Estimated off-take as a percentage of total population has been indicated to diverge widely between species. Among several resident species in Africa, including giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*) and topi (*Damaliscus korrigum*), off-take must be considered high. For instance, past exploitation for bush meat in Serengeti has significantly reduced the Cape buffalo (*Syncerus caffer*) by 50-90% in parts of their range and local declines in waterbuck (*Kobus ellipsiprymnus*) and giraffe population (Campbell, 1989; Dublin et al., 1990). Furthermore, roan antelope *Hippotragus equines* might have never been common in Serengeti due to over hunting (Turner, 1987; McNaughton, 1989). Hippo (*Hippopotamus amphibious*) populations are not known in many ecosystems, thus the effect of off-take is difficult to assess (Hofer et al., 1996). Furthermore, Rusch et al. (2005) reported a drastic decline in the topi population in Serengeti, while populations of other herbivores either remained steady or increased which raises concern that the topi is particularly targeted by illegal hunters and exploited at unsustainable level. In Zambia, a comparison between the 1960s and 1994, animal sighting close to the villages suggest a drop of 50% of hippo populations (Marks, 1994). Moreover, a long term study from Ghana suggests that bushmeat hunting caused a decline of about 41 species of mammals by 76% between 1970 and 1998 and a local extinction of between 16 to 45% of the same species (Brasheres et al., 2001).

Some previous studies suggest that illegal hunting, which is the major source of bush meat supply, has been more detrimental to animal population not only for bush meat species but also for trophy animals. For instance, unchecked illegal hunting between 1975 and 1986 drove the black rhino (*Diceros bicornis*) populations to factual extinction and significantly reduced the elephant population size in Tanzania (Hofer et al., 1996). In Kenya, black rhino population decreased by 90% between 1969 and 1979 whereas in Zambia the black rhino population decreased from 12 000 individuals in 1972 to a few hundred in the 1980s (Leader-Williams & Albon, 1988). Untargeted species has also been caught in snares set for bush meat. In the Serengeti for instance, 8% of spotted hyenas (*Crocuta crocuta*) from the study population of 423 individuals are killed each year by snares that are set for bush meat (East and Hofer, 2000).

Dietary contribution of bushmeat to local people

Generally, the main factors attributing to high consumption of bushmeat is local availability, easy catch-ability (wire snares, pitfall traps), affordability and the consequent household savings. Snares and pitfall traps are easy to set and very efficient, while it is easy to conceal (Paper I). Moreover, bushmeat is usually cheaper than meat from livestock. For example, in Kitui district, amounts of bush meat consumed equate to 34% of household monthly income and from 15.7% to 39.2% in Kweneng and Kgalagadi in Botswana, respectively (Barnett, 2000).

In Tanzania for example, illegal utilization of bushmeat represents a larger economic value of wildlife than legalized trophy hunting or photographic tourism (Barnett, 2000). A current study in Serengeti indicates that 83% of households buy illegal bushmeat (Holmern et al., 2004) the majority of them are subsistence farmers (Loibooki et al., 2002). The estimated mean number of people per household in the western Serengeti is seven (Hofer et al., 1996). Considering the number of households within 45 km from the park boundary, i.e. 137,750 households (roughly 964,250 people) depend on bushmeat as their main animal protein in the area with about 1.37 million people (URT, 2002). Annual off-take from this part of Serengeti alone has been estimated as 159,811 wild animals including resident (28%) and migratory species (72%) (Hofer et al., 1996). This is equivalent to 11,950 tons of meat per year or 230.6 g of meat per person per day.

In other African countries like Zambia, a similar study shows that a total of 27.4 tons of meat was made available to 466 local residents during the course of a year (Marks, 1973).

This is equivalent to 162 g of meat per person per day. Consumption of bush meat from these two regions surveyed is much higher than the minimum Food and Agriculture Organizational (FAO) recommendation of 60 g meat per person per day (Barnett, 2000). However, in Zambia, bush meat off-take for commercial purposes was considered to replace trophy poaching as the main impact on wildlife populations in many areas (Marks, 1973; Marks, 1994).

A study of bushmeat utilization in Kenya suggests that bushmeat represents the bulk of all meat protein consumed by Kitui communities. The study observed domestic meat playing a reduced role in meeting protein requirement as the meat from livestock was expensive (Barnett, 2000). Furthermore, study indicates that 80% of households consume 14.1 kg of bushmeat each month. In addition, FitzGibbon et al. (1996) report that traditional hunter or gatherer forest dwelling people rely heavily on bush meat as protein and potential income generating activity. In Botswana, 18.2 kg of bush meat is consumed per household per month by 46% of the Kweneng local people and the meat was the only viable source of meat protein for many rural inhabitants living in the semi-arid range land of the country (Barnett, 2000). Assuming an average of 7 people per household (Hofer et al., 1996), the average amount of meat consumed per person per day would be 86.7 g. This, however, is still higher than the minimum FAO recommendation. In Maputo Mozambique, the study indicates that more than 50 tons of bushmeat is traded per month. This has attributed directly to a severe decline in wildlife populations in the area. In Malawi the mini-fauna species are presently the source of meat protein to the majority of people (Barnett, 2000).

In contrast to countries within the Congo basin, the bush meat intake per day in Gabon and Congo were 180g and 89g, respectively (John et al., 2003). Likewise, these intakes were still higher than the minimum amount recommended by FAO. However, within the region, the study indicates that Cameroon and Democratic Republic of Congo (DRC) had much lower bush meat intake per person per day of 26g and 28g, respectively (John et al., 2003) suggesting depletion of the resource in these areas.

Aims of the thesis

This thesis evaluates the conflicts between human and wildlife in the human-wildlife interface using the western section of the Serengeti ecosystem in Tanzania as a case study. The first part of the thesis focuses on the conflict related to utilization of natural resources and livestock depredation (Papers I-III) whereas the second part focuses on the dietary contribution of bushmeat to local people, bushmeat experience and utilization (Papers IV-V).

METHODS

Study area

The study area is located in the north-eastern corner of Tanzania (Fig 1) on the north-western part of Serengeti National Park (SNP) (14 763 km^2). The SNP is the central part of the greater Serengeti Ecosystem in the northern Tanzanian highlands. Serengeti was declared a national park in 1951 and a World Heritage Site in 1981 when the bordering Ngorongoro Conservation Area became a Biosphere Reserve. The park is approximately one-half of the entire ecosystem, which includes the Ngorongoro Conservation Area, Maswa, Ikorongo, Grumeti Game Reserves, Loliondo Game Controlled Area, and Masai Mara Game Reserve in Kenya (Fig 2).

The Serengeti ecosystem is a highland savannah region with thorn tree woodlands and plains from approximately 900–1500 meters above sea level. Annual precipitation ranges from about 800 millimetres in the east to 1000 millimetres in the northwest (Norton-Griffiths et al., 1975). The world largest populations of herbivores and carnivore are found in this ecosystem and the majority of the species of the East African savannah are found there too. Serengeti is famous for the large scale herbivore migrations (wildebeest, Thomson's gazelle, zebra and eland, Fig 2) as well as for the large populations of resident herbivores (African buffalo, giraffe, Grant's gazelle, impala, topi, warthog (*Phacochoerus aethiopicus*), and waterbuck). Sizeable populations of large carnivores like lion, leopard, cheetah and hyenas also roam these areas (Sinclair, 1995).

The people inhabiting this region are either agro-pastoralists or pastoralists. The areas north and west of SNP are densely populated (> 70 people/km^2, human population in Mara Region was about 1.37 million growing at a rate of 2.9% per annum (URT 2002)) by a diversity of tribes and ethnic groups. The main tribes are Ikizu, Zanaki, Sukuma, Jita, Taturu, Ikoma, Kuryia, Natta, Issenye and Luo. In earlier years, the cultural and ethnic differences were much more distinct than they are today. Largely due to the rapid population growth and significant transmigration from other areas far from the park boundaries, most of the communities along western Serengeti are currently multiethnic. The communities are organised just as much around available space and agricultural land and the search for economic opportunities, as traditional culture.

The average annual cash income of local people living in the study area is low (i.e. US$ 140 in 2001, Borge, 2003). Overall, Tanzania is a poor country with a per capita income of US $ 280 (World Bank 2006). By most conventional standards the villagers residing around north-western Serengeti are impoverished, and a great number of them qualify as poor by the UN standard. The main economic activities include farming and livestock production. Farming is mostly based on crops like cassava, sorghum, millet, maize (food) and cotton (cash crop). The crops cycle follows the rain-pattern with long rain lasting from March-May and short rain October-December. January-February and June-September are always dry. Maize, sorghum and millet are planted twice a year; in February-March and August-October and harvesting period is between June and July and between January and February, respectively. Livestock includes cattle, goats, sheep and poultry, although few households keep pigs and donkeys. Hunting varies in importance among these tribes. The wildebeest migration is a central part of the annual life cycle for tribes like Ikoma and Kurya where hunting has traditionally been a part of culture and life patterns. The estimated number of illegal bushmeat hunters within 45 km of SNP and adjacent protected areas is 23,294 and 31,655, respectively (Campbell and Hofer, 1995). A more recent estimate (Campbell et al. 2001) puts the number of illegal bushmeat hunters at approximately 60,000, i.e. an increase of 90% in ten years (from 1988 to 1998). In contrast, the population to the east of the park is dominated by pastoralists (Maasai, who supposedly do not hunt), and there is very little farming here.

Illegal bushmeat hunting and law-enforcement

In the western Serengeti illegal hunting has increasingly become a coping strategy for a major part of the population as legal access to resources has been restricted (Campbell et al., 2001). According to Loibooki et al. (2002) people of the western Serengeti participate in illegal hunting in order to offset food shortage and generate cash income. Participation in illegal bushmeat hunting decreased with increasing numbers of livestock owned, and people with access to alternative income means were also less likely to engage in illegal hunting. Furthermore, involvement in illegal hunting was not reduced by participation in community-based conservation programmes.

In Serengeti, anti-poaching patrols have been an important task for park staff since the inception as a national park (Arcese et al., 1995; Loibooki et al., 2002). Arcese et al. (1995) report a possible six-fold increase in arrests from 1957 to 1991. However, they also point out that the ranger force has doubled since 1963, and in order to understand the changes one must know how many people actually enter the park to hunt. Given the contentious nature of the issue, it may be impossible to arrive at an accurate estimate of this figure, at least if it is based on observation and self-reports.

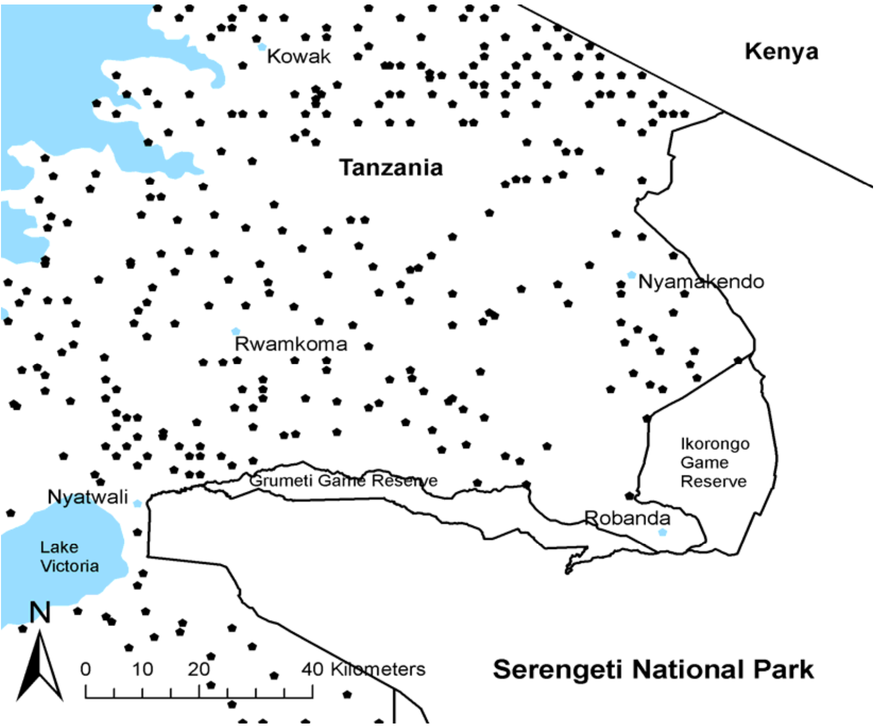

Figure 1: Map of the western Serengeti showing the location of some study villages (Robanda, Nyamakendo, Nyatwali, Rwamkoma and Kowak) and the surrounding villages (Black dots).

Off-take levels

The illegal hunting activity has been spatially modelled. Campbell and Hofer (1995) estimated that in and around Serengeti 210 000 herbivores are hunted illegally each year. Of this, wildebeest comprises 57 per cent (118 922 animals). However, Mduma et al. (1998) estimated a much lower number of 40 000 wildebeest illegally hunted each year, and predicted that a harvest of 80 000 animals per year is unsustainable and could cause a total collapse of the wildebeest population by 2018. Given the fact that the current wildebeest population is reasonably stable at approximately 1.3 million animals could indicate that the Campbell and Hofer (1995) estimates may be too high.

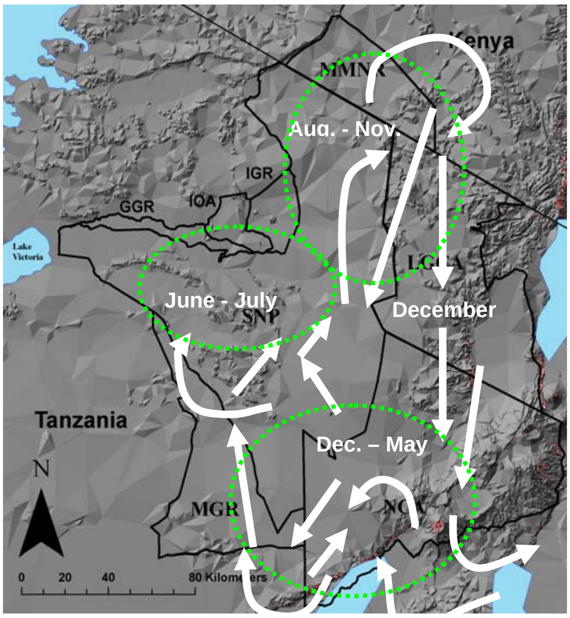

Figure 2. Map of the Serengeti ecosystem. The core area is Serengeti National Park (SNP), surrounded by Maswa Game Reserve (MGR), Grumeti Game Reserve (GGR), Ikorongo Game Reserve (IGR), Maasai Mara National Reserve (MMNR), Loliondo Game Controlled Area (LGCR) and Ikoma Open Area (IOA). The arrows show the movement of wildebeest around the Serengeti Ecosystem. The wildebeest usually carves in the southern short grass plain in December-February each year. The northern part of the ecosystem is the refuge of migratory herbivores during dry season (August-November). On their northward migration (May-July), the wildebeest herds use parts of the western corridor, as well as the adjacent game reserves and open village lands, depending upon the rainfall pattern (adapted from Thirgood et al., 2004 and Rusch et al., 2005).

Hunting techniques

Hunting is conducted in a number of ways. Few people own firearms so most illegal hunting is accomplished by setting snares and pitfall traps (Plates 1 and Plate 2). Snares and pitfall traps are unselective hunting methods and can injure or kill a wide range of animals from large carnivores to small and large herbivores. They are often inefficient in killing and animals may suffer for a long time before they are dealt with by hunters and/or sometimes die and scavenged by predators (Plate 3). In some cases an animal escapes with a snare wire deeply cut through the neck (Plate 4). In some cases hunting involves well organised parties on several week long expeditions into the bush where the hunters set up a secluded camp, butcher and sun dry the meat before they depart. Much of the meat is then preserved in a form (swahili: 'kimoro') that permits storage and selling or trading in markets locally or far away (Kaltenborn et al., 2005). Alternatively, smaller groups and individuals take what they can find in their immediate surroundings, and mostly for subsistence use. During the wildebeest migrations huge herds of animals roam through villages and agricultural lands and great numbers of animals are slaughtered literally at the doorstep. A few authors have attempted to quantify the economy linked to wildlife harvesting (Campbell et al. 2001; Borge 2003), but there is as yet no comprehensive picture or consensus neither on the magnitude of the harvest, nor on the contribution to rural household economies due to the delicacy of the subject to local communities.

Plate 1: Snare wire set ready waiting for the victim in the park section of Ndabaka plain (Photo: J. Nyahongo)

Plate 2. Pitfall trap in Serengeti National Park (Ndabaka plain): big enough to swallow a mature buffalo (Photo: J. Nyahongo)

Plate 3. The scavenged victim of wire snare (Photo: J. Nyahongo)

Plate 4: A lioness with a wound around neck that has been inflicted by a wire snare (Kirawira pride) (Photo: J. Nyahongo)

Study species

In this study, we include those wild animals that influence human livelihood (bushmeat) and livestock (depredation). In the western Serengeti, the wildebeest, zebra and Thomson's gazelle migration has large impact on the livelihood of local communities adjacent to park boundary. However, resident animals such as topi, giraffe, impala, buffalo, warthogs and waterbuck are important sources of meat for both human and large carnivores (lions, spotted hyena and leopard) in the area. Spotted hyena is the most numerous carnivores in the area and the species is also found outside the protected areas. Thus, this is the carnivore being mostly involved in livestock depredation.

Data collection

Data for this thesis were collected during several field trips. Data on the benefits and costs of illegal grazing and hunting (Paper I) was collected between May 2001 and March 2002 for livestock depredations (Paper II) was collected between September and November 2004. Data for livestock depredations (Paper III) and for bushmeat utilization (Paper IV and Paper V) was collected between January and December 2006 (See the respective papers for detailed complete descriptions of methods).

MAIN RESULTS

The following papers (I, II & III) focuses on the conflict related to utilization of natural resources and livestock depredation.

Paper I

The levels of illegal use of natural resources by local communities surrounding the western Serengeti were influenced by the likely value of the resources acquired and the probable costs associated with their acquisition. Evidence of hunting was found in the national park section closer to a ranger post, suggesting that benefits (bushmeat) of hunting mostly outweighed costs (chances of being arrested) in these areas. However, the level of illegal hunting was observed to decrease with the distance hunters have to travel on foot to hunting areas. Travel cost is likely to be assessed not only in terms of distance travelled but also in terms of time that could be devoted to other activities (opportunity cost). In contrast, despite the high densities of livestock close to the boundary of the protected areas, livestock was rarely illegally present inside these protected areas. This may indicate that livestock owners considered the chance of detection (as it is difficult to conceal grazing livestock) and likely financial penalties (when livestock are confiscated) too high in relation to the benefit gained from illegally acquired forage and the use of watering areas inside the areas.

Paper II

Livestock depredation in the villages surrounding the western Serengeti is mostly caused by spotted hyena, followed by leopard, baboon (*Papio cynocephalus*), lion and jackal. Economically, the livestock depredation contributed to two-thirds of the annual cash income for the households in the study area. This does not only intensify the human-carnivore conflicts but also may be a serious obstacle to both human and livestock development. Depredation events were not only reported to villages close to the protected areas but also affected households in distant villages where only the spotted hyena was reported to be involved in livestock killings. Lion and leopards only killed livestock in the households that were close to protected areas. Tolerance of livestock depredation was low and the majority of livestock owners accept retaliatory killing as a way to reduce loss. Level of education, the number of livestock previously lost and the perceived effective protective measures had influence on acceptance of retaliatory killing.

Paper III

Among the recorded causes of livestock losses such as disease, depredation, theft, and loss in bush while grazing, the results suggest that diseases are responsible for the highest loss. Death of livestock due to diseases affected household similarly. Overall, diseases cost was 59.6% of average annual household cash income. In comparison, the contribution of diseases to livestock loss was four times higher than depredation in the household located far away from the park boundary, and was about 10 times higher than the cost of depredation in the households that were close to the park boundary. More sheep were killed by spotted hyena in the households located farther away than those located close to the park boundary. Overall, spotted hyena killed more sheep than goats or cattle.

The following papers (IV & V) focuses on the dietary contribution of bushmeat to local people, bushmeat experience and utilization.

Paper IV

Meat and fish meals per household were studied in villages that were located close, intermediate and/or farther away from the boundary of the protected areas (Serengeti National Park and Grumeti-Ikorongo Game Reserves) and/or the Lake Victoria. Generally households that were close to the protected areas consume more meat during the migration than those located farther away where the peak meat consumption in the villages close to protected areas corresponded to the peak influx of migratory herbivores. Similarly, households located close to Lake Victoria eat more fish than those located farther away. The consumption of fish meals is not affected by the influx of migratory herbivores close to the villages located close to the lake. Fish consumption in villages that were close to the protected areas but far from the Lake Victoria declined with the influx of migration. The household income significantly influenced the meat consumption in the villages that were far from the protected areas but not in the villages that were located close or intermediate distance from the boundary of the protected areas.

Understanding human species preference and ability to recognize species by meat taste may be employed to explore how some group of people along the gradient of distance from the park have experience with different species of wild ungulates and beef. This can be an indirect method to evaluate the levels of the past and current bushmeat utilization.

Paper V

Our overall results show that test-persons favoured beef, followed by topi and impala. The preference patterns and the ranking position of beef, topi and impala alternated along the gradient of distance from the park suggesting high preference and acceptability of the three species by test-persons from different villages along the gradient of distance from the park boundary. Moreover, it was possible to predict the preferences of beef, topi, impala and wildebeest along the gradient of distance from the park. In contrast, the results indicated that most test-persons were not able to identify the species based on the meat test. Generally, the most correctly identified meat was beef while the least identified species was impala. Age and gender did not have a significant effect on meat preference for all species in the pooled data. Distance from the park had a negative effect on the preference of topi and the similar effect on the identification of all five species studied suggesting a different level or type of experience with topi in the immediate villages.

DISCUSSION

Natural resources utilization and wildlife experience

Generally the findings from this study show that local people living close to protected areas are rational when it comes to the illegal utilization of natural resources. They consider the benefits and cost of illegal utilization of natural resources (Hofer et al., 2000;

Paper I). In this context, local people living close to protected area are able to plan and carefully follow the laid plans during the hunting operation. They know in advance which areas in the protected areas are profitable (high herbivore densities), at the same time they consider the cost (chances of being arrested and the distance to walk). While illegal hunting can take place far inside the park, livestock keepers avoid grazing deep inside the national park because they know the consequences (penalties and fines) of utilizing the pasture in the park illegally. Illegal hunting can be easily concealed and often takes place at night while grazing take place during the day and involves large herds of cattle, which is easier to see from long distances. In the western Serengeti previous studies indicate that most arrested illegal bushmeat hunters are poor uneducated people who own few or no livestock (Loibooki et al., 2002), which suggest that bushmeat hunting has been and will continue to be (unless the economy and social services such as better education, employment opportunities, health and water sanitation are improved in the villages) a coping strategy for survival in the areas with relatively abundant wild ungulates (Kaltenborn et al., 2005).

In order to investigate the dietary contribution of bushmeat to local people and their experience with wildlife as a result of long term human-wildlife interactions (bushmeat utilization), one method we can use is direct and indirect observation of what local people consume during the period spanning several months or years and compare that with the seasonal movements of migratory herbivores through and around the Serengeti ecosystem. On their northward migration, wildebeest moves close or direct in village areas during the period covering about three months (May-July) each year. During this period, substantial numbers of wildebeest and zebra are slaughtered for bushmeat.

The findings of the current study (Paper IV) shows that local people living close to protected areas consume more meat meals during the period when the wildebeest are in the village proximities than when the herds are far into the southern plains. This further proves the rationality of illegal bushmeat hunters when planning for hunting trips (the benefits versus cost). In contrast, the fish meals in the villages located close to protected areas but far from the Lake Victoria decrease with influx of migratory herbivores, which suggest that fish and meat complement each other when the distance from the sources fluctuate (because fish must be bought and expensive when compared to bushmeat that may be obtained freely or very cheap from the illegal bushmeat hunters during the influx of migratory herbivores).

Local people switch to more available and inexpensive sources of protein whenever the opportunity comes (Barnett, 2000; Brashares et al., 2004; Rowcliffe et al., 2005). In the distant villages (> 80 km), the meat and fish meals depended on the household income and not the movement of migratory herbivores around the Serengeti ecosystem. This was proved when test-persons from villages close, intermediate and distant from the nearest park boundary were given pieces of meat in a combination of wild ungulates and beef to rank the meat according to the perceived taste. In addition, the test-persons were requested to recognize the species of animal whose meat they tasted. Villages that were close to park boundaries as well as those in the intermediate (< 43 km) areas preferred topi and impala, respectively. The test-persons from distant villages preferred beef to all other species, which suggests long term experience with beef as no other source of meat is locally available in the area other than livestock meat. In contrast, test-persons from the villages that are located at short or intermediate distance from the park may have different experience with different species of wild ungulates and preferred some meat over others although overall preferred meat was beef.

Conflicts over livestock depredation

Human-carnivore conflict over livestock depredation is a serious management issue often causing opposition towards conservation at a worldwide scale. The results from the current study in the villages surrounding the western Serengeti show that among the wild carnivores reported to kill livestock, 97.7% of reported species was spotted hyena, being responsible for 98.2% of total livestock loss (US $ 12,846 in 2003) (Paper II). The killing was not only restricted to villages in the proximity of the park but also as far away as 80 km (Paper III). The most numerous large carnivore species in the Serengeti ecosystem is the spotted hyena (Mill and Hofer, 1998). Thus, it is not surprising that this is the species of carnivore villagers in the study area report to attack livestock most frequently. Given that this species is mostly a nocturnal predator, it is also to be expected that most attacks by this species occur at night. In the study area, livestock is taken out from the village to graze during the day, and then kept in enclosures or bomas, usually close to houses, at night. In addition, the nocturnal and opportunistic foraging behaviour, together with the ability of spotted hyena to take long distance commuting trips, make them particularly adaptable to anthropogenic environments (Kruuk, 1972; Hofer and East, 1993; Mills and

Hofer, 1998). Livestock keepers show no tolerance towards carnivores that kill livestock. The analysis shows that level of education associates with higher levels of tolerance, while for livestock keepers higher depredation rates is linked to approval of lethal retaliation and effective protection measures is associated with a reduced desire of retaliation. However, the negative attitudes towards large carnivores may be due to human safety as well (Kalternborn et al., 2005; Packer et al., 2005; Røskaft et al., 2007). Our study that included households in the villages that are close and distant from the park boundary indicates that goat and sheep are targeted by hyena and that more killings were recorded in the households farther away from the boundary of the park than in the households in the park proximity (Paper III). This suggests an existence of the spotted hyena in the area with high anthropogenic activities. However, the data collection period was not sufficiently long to warrant the fair comparison and because I only had one village far away from the park boundary, the results may also be a result of pseudoreplication. Moreover, the sample size in distant villages was not large and extensive enough for representing the conclusive picture on the livestock depredation. This is because the depredations recorded may involve one animal or a single group of animals.

When the level of loss due to diseases was compared to loss due to predation, diseases caused higher livestock loss in households than depredation, theft or loss while grazing. This observation is in agreement with other studies conducted elsewhere (Ogada et al. 2003; Frank et al., 2005; Kolowski and Holekamp, 2006; Holmern et al., 2007). Disease, although farmers in Africa do not consider it seriously (Mwangi, 1997), were responsible for 3.5-7.0% livestock loss per household during the period of nine months, costing them US$ 83.5 (Paper III). This loss is equivalent to 59.6% of the average annual household income (Borge, 2003). The cost per household of theft and poor management in the grazing field was US $ 3.0 and US $ 11.4, respectively. The cost of depredation recorded was higher in the household located far away from the park boundary. The depredation cost per household in the four villages was US$ 16.5. Livestock keepers may not observe the direct effect of diseases to their livestock production due to the fact that the sick animals may be slaughtered and used as food or sold to neighbours while carnivores often consume all edible parts of a kill; leaving nothing to human consumption. Moreover, diseases often kill larger number of new born calves than adults (personal observation, 2006).

Due to poor livestock husbandry skill (records), livestock keepers may not observe this as an important loss because the capital investment in terms of veterinary service, feeding or grazing time and/or output in terms of meat or money (when sold) is relatively much lower for new born calves than for adults, although the new born calves are the future mature animals. The problem with carnivores is the level of economic loss caused in a single attack. This is because when a carnivore breaks into the livestock enclosures, usually at night (Nyahongo, 2004; Kolowski and Holekamp, 2006; Holmern et al., 2007), it may kill several adult livestock. However, since the compensation scheme that may offset some of the costs are always lacking in Tanzania, negative attitudes towards carnivores may have developed among farmers and which have resulted in retaliatory killing of carnivores in or close to village proximities (Holekamp and Smale, 1992;

Ogada et al., 2003; Dickman, 2005; Frank et al., 2005; Graham et al., 2005; Holmern et al., 2007).

MANAGEMENT RECOMMENDATIONS

Based on my findings and the experiences from other studies in similar ecosystems, I recommend the following:

i) Improvement of primary and secondary education in village schools in rural areas with the emphasis on wildlife conservation programs in the areas adjacent to protected areas. Education may improve attitudes of local communities towards carnivores (Lindsey et al., 2005; Woodroffe et al., 2005; Røskaft et al., 2007).

ii) This study suggest that local people would benefit from better education on animal husbandry practices and extension service to help them maintain the health of their livestock and to prevent theft and loss of livestock while grazing. I recommend that diseases control and management should be integral part of regional and national programs to limit disease transmission between livestock and wildlife and even among livestock in the villages.

iii) To conserve the carnivores outside the protected areas, a change in wildlife policy to allow compensation when livestock are killed by wild predator may be required this could contribute to the changing of the negative attitude that exists among livestock keepers towards wild carnivore. That may reduce retaliatory killings of such carnivores commuting from protected areas or that taking refuge in the few remaining thickets, kopjes, hills and/or mountains that are located within the village areas.

iv) I suggest that night enclosures for livestock should be improved to reduce the conflict due to livestock losses between local people and wild carnivores. However this would require considerable effort in terms of hours of work, and might require some financial investments.

v) In order to reduce the dependence on bushmeat, alternative sources of meat protein like aquaculture together with some income generating projects such as poultry and horticulture need to be considered in both general local as well as national development planning.

vi) The contribution of fish to household diet as an alternative to bushmeat should be emphasized so that the limitation on processing fresh fish and transportation to local market is solved. Industrial harvesting of fish from Lake Victoria need to be coordinated as it may reduce availability of fish to the local markets in both villages located close to the lake and the distant villages from the lake and thus increasing pressure and reliance on bushmeat around the lake region.

vii) The increased reliance on bushmeat may have negative impacts on the resident herbivore populations. Thus, the policy markers need to understand the link and the need for coordinated management between these two ecologically very different resources; the bushmeat species and the fish.

viii) The price of beef should be reduced and wildlife management somehow should manage to limit bushmeat supply (preferably by cooperating actively with communities) so that many people may choose to eat more beef rather than wild ungulates. This will inevitably reduce the hunting pressure on resident herbivores.

ix) The findings from this thesis suggest the need for special conservation attention to resident herbivore populations close to village proximities. Otherwise the long term harvest and uncontrolled illegal bushmeat hunting based on current meat preferences and habitat location may seriously deplete the resident herbivore species from their key habitats.

FUTURE RESEARCH NEEDS

Future studies on the effect of bushmeat processes before transportation to the market place is recommended. This is important because the bushmeat consumers may be used to sun-dried meat that may influence the fatty aroma and the texture in different levels among the different species.

Further research on the coping strategies for supplementing the low meat protein consumption in the villages located farther from the park needs to be carried out. This is important for advising local communities living close to the park boundaries on such alternative sources of protein so that they reduce reliance on bushmeat

The findings from this study suggest further research on the population ecology of wild carnivores outside the protected areas in order to establish the current coping strategy of these carnivores and possible current spatial-temporal conflicts resulting from the interactions between human and the carnivores.

Further research on the nutritional contribution of bushmeat to local communities in the western Serengeti and the consequences on both bushmeat species and humans in the future depending on the increasing human population is recommended.

Study on the alternative income generating projects that are socio-culturally acceptable and environmentally friendly such as beekeeping, poultry, aquaculture and horticulture is recommended in order to help in alleviating poverty among local people in the western Serengeti.

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Paper I

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Benefits and costs of illegal grazing and hunting in the Serengeti ecosystem

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SUMMARY

Two forms of natural resource use (meat hunting and livestock grazing) were investigated at three sites in the western region of the Serengeti ecosystem, Tanzania. Statutory management of natural resources in this region was designated as National Park, Game Reserve or village council. A quasi-experimental design examined factors likely to alter the cost and benefit of illegal use by ranking areas within sites in relation to these factors. Factors likely to alter costs were the chance of arrest, determined by the presence or absence of guard posts, and the distance travelled to the site of exploitation. As all sites experienced large fluctuations in the density of migratory herbivores, it was assumed that the benefit acquired from hunting increased with wild herbivore density. Marked seasonal changes in precipitation were considered likely to alter the value of forage and water to livestock owners. Hunting effort (density of snares) increased as the density of wild herbivores increased. The distribution of hunting effort across sites was more consistent with the prediction that high travel costs were more likely to curtail hunting than a high potential cost of arrest. Unlike hunters, livestock owners mostly avoided the use of resources in protected areas probably because of the high potential cost of arrest and confiscation of stock. Natural resources within protected areas were exploited when benefits outweighed likely costs.

Keywords: illegal hunting, livestock grazing, natural resources, Serengeti ecosystem

INTRODUCTION

Hunting of wildlife to obtain meat for subsistence or trade is important to local economies and a growing problem for wildlife managers in many countries (Arcese *et al.* 1995; Campbell & Hofer 1995; Fa *et al.* 1995; Barnett 2000; Loibooki *et al.* 2002; Rao & McGowan 2002). The extent to which wildlife populations in Africa are used for meat is high in terms of the number of animals killed and the volume of meat obtained (Hofer *et al.* 1996; Mduma *et al.* 1998; Noss 1998; Barnett 2000). This offtake is mainly achieved through the use of inexpensive methods of prey capture, such as wire snares, self-made traps and poisoned darts or arrows (Turner 1987; Noss 1998), and the use of non-selective capture methods such as snares has a negative impact on populations of non-target species (Hofer *et al.* 1993). The most ubiquitous hunting method is the wire snare, probably because snares cost little and are relatively simple to make; thus hunters can afford to own and set numerous snares. Once set, snares are inconspicuous and law enforcers in areas where hunting is illegal find them difficult to detect.

Use of forage and water can produce conflict between managers of protected areas and local communities (Fleischner 1994; Arcese *et al.* 1995; Homewood *et al.* 2001; Madhusudan 2004; Mishra *et al.* 2004). In comparison to illegal hunting with snares, livestock ownership requires greater financial expenditure and the illegal presence of livestock in protected areas is more difficult to conceal.

The Serengeti ecosystem straddles the international border between Tanzania and Kenya. The major part of the ecosystem lies within the Serengeti National Park (Serengeti NP) where hunting of wildlife and grazing of livestock are prohibited. Situated along sections of the Serengeti NP boundary are game reserves, where licensed hunting is permitted but livestock and unlicensed hunting are prohibited. These reserves form a buffer zone between the Serengeti NP and surrounding communities.

Given that over one million people live within 45 km of the western boundary of the Serengeti NP and associated reserves (Campbell & Hofer 1995), and that the main occupation in the area is subsistence farming plus the rearing of livestock (Loibooki *et al.* 2002), it is perhaps not surprising that natural resources within the protected areas are used by local communities (Arcese *et al.* 1995; Campbell & Hofer 1995; Hofer *et al.* 1996; Loibooki *et al.* 2002). The level of illegal hunting for meat is considerable and has resulted in the local extinction of resident herbivores in some areas (Arcese *et al.* 1995; Campbell & Hofer 1995; Hofer *et al.* 1996). Livestock ownership is viewed as a symbol of wealth and status, and inhabitants of villages close to the Serengeti NP that either own livestock or have access to alternative means to generate income and acquire protein are less likely to participate in illegal hunting (Loibooki *et al.* 2002). The link between poverty and illegal meat hunting is also reflected by the fact that illegal hunters arrested in the Serengeti NP were

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predominantly poorly educated, young males that owned few or no livestock (Loibooki *et al*. 2002).

This study aims to build on previous research in the Serengeti ecosystem on how costs and benefits of illegal hunting influence the spatial and temporal distribution of this illegal activity (Arcese *et al*. 1995; Campbell & Hofer 1995; Hofer *et al*. 1996, 2000; Loibooki *et al*. 2002). Here we compare illegal hunting and illegal livestock grazing to investigate whether the spatial distribution of these activities is consistent with the expectation that natural resources within protected areas will be exploited when likely benefit exceeds estimated cost and to assess which component of cost is likely to matter the most.

METHODS

Study area

The study was conducted in the western section of the Serengeti (Tanzania). The economy of local communities was mainly based on subsistence agriculture with more prosperous farmers owning herds of livestock (Loibooki *et al*. 2002). An average herd of livestock in 2001 consisted of 17 animals that had a total sales value of US$ 423–735 (Loibooki *et al*. 2002). Inhabitants of villages close to Lake Victoria practised commercial fishing, and those in villages close to all-weather roads practised commercial trade (Loibooki *et al*. 2002).

Illegal hunters from local communities chiefly used wire snares to capture wild herbivores for meat that was typically dried before being carried on foot from protected areas (Arcese *et al*. 1995; Hofer *et al*. 2000). Dried meat was used for home consumption, sold to generate income or bartered for other commodities (Hofer *et al*. 2000; Loibooki *et al*. 2002). An estimated 53 000 people are involved in illegal hunting, including both hunters and porters that transport meat from hunting camp out of the protected areas (Loibooki *et al*. 2002). Hunters arrested in the Serengeti NP come from villages within 45 km of the boundary of the protected areas (Campbell & Hofer 1995). Although a large proportion of the annual offtake of meat from the ecosystem is obtained from large migratory species such as wildebeest *Connochaetes taurinus* and zebra *Equus burchelli*, considerable volumes of meat are also obtained from other migratory and resident herbivores species (Arcese *et al*. 1995; Hofer *et al*. 1996). It is not known what proportion of illegally hunted meat is sold for cash, used for home consumption, or bartered for other commodities. For this reason it is difficult to estimate the monetary value of this illegally acquired commodity to the local economy, even though it is undoubtedly important economically (Loibooki *et al*. 2002). If only a third of the estimated annual offtake of approximately 11 950 tonnes of useable meat (Hofer *et al*. 1996) from migratory and resident herbivore species is sold (at a value of US$ 0.3 per kg fresh weight of meat; Loibooki *et al*. 2002), trade in illegal meat would annually generate more than US$ 1 million.

Density of wild herbivores, livestock and snares

Between May 2001 and March 2002, data were collected along ground transects in three areas, namely Kirawira, Mihale and Ndabaka. The Kirawira transect was entirely within the Western Corridor section of the Serengeti NP, two ranger posts both within 1 km of the transect being staffed by a total of 14 rangers. From each ranger post, six rangers patrolled by vehicle and on foot, and one ranger provided patrols with radio communication. There were frequent tourist vehicles in the area, many of which could communicate by radio with the ranger posts. This site was a greater distance from the boundary of the protected areas than the other two study sites. The Mihale transect was on the northern side of the Western Corridor that traversed an equal distance of the Serengeti NP, the Grumeti Game Reserve (Grumeti GR) and the unprotected area outside this Reserve. The Serengeti NP section of this transect was at a greater distance from the protected area boundary than the section of this transect in the Grumeti GR. The nearest ranger post was approximately 15 km from this transect. Grazing of livestock and unlicensed meat hunting were prohibited in the Grumeti GR. Although licensed trophy hunting was permitted within the Reserve, during the study no trophy hunters operated and tourists rarely visited the area. Natural resources outside the Grumeti GR could be legally exploited. The Ndabaka transect was on the southern side and at the western end of the Western Corridor, within 3 km of a ranger post and entrance gate to the Serengeti NP that was staffed by five rangers (three patrolled, one administered the entrance gate, and one was responsible for radio communications). Two-thirds of this transect was within the Serengeti NP and one third was in unprotected land outside the Park. As there was no reserve to act as a buffer zone between the Park and local communities, the distance from the boundary to the section of this transect inside the Park was small.

Each of the three study sites contained a 45-km transect composed of three parallel 15-km transects situated 4 km apart. Transect lines and the location of the National Park and Game Reserve boundaries along transects were determined by a global positioning system (GPS; Garmin 12 XL). A vehicle with a driver and an observer was slowly driven along each transect. In the three study sites, each 45-km transect was driven three times per month for 11 months. The numbers of livestock (cattle, goats, sheep and donkeys) and wildlife observed within 200 m either side of the transect line were counted and the GPS positions recorded. The herbivorous species counted during transects included wildebeest, zebra, eland *Taurotragus oryx*, Thomson's gazelle *Gazella thomsoni*, Grant's gazelle *Gazella granti*, topi *Damaliscus lunatus*, impala *Aepyceros melampus*, buffalo *Syncerus caffer*, giraffe *Giraffa camelopardalis*, kongoni *Alcelaphus buselaphus*, and warthog *Phacochoerus aethiopicus*. All these species are hunted and can be caught by wire snares.

Snares within 20 m of either side of a transect line were recorded. The GPS position of snares was taken and snares were inconspicuously marked with a permanent pen to prevent recounting previously logged snares at a later date.

The densities of wild herbivores, snares and livestock were calculated for each study site using the equation (Caughley & Sinclair 1994):

$$D = \Sigma x / \Sigma A, \qquad (1)$$

where D is the calculated mean density of livestock and/or hunting equipment counted, Σx is the sum of mean livestock and/or hunting equipment counted per month, and ΣA is the sum of the mean area covered during the count.

All three sites experienced a similar pattern of precipitation, with the majority of the annual precipitation falling between November and May (the 'wet season') and little precipitation between June and October (the 'dry season').

Mihale village was approximately 5 km from the Mihale transect and, in 2001, contained 1036 people that owned 0.53 sheep or goats per person and 0.65 cattle per person. Mwabayanda village was within 5 km of the Ndabaka transect and, in 2001, this village contained 2771 people that owned 0.50 sheep or goats per person and 0.99 cattle per person. These two villages were of roughly similar size and were comparable in the number of livestock owned per head, which is an index of village wealth (Loibooki *et al.* 2002).

We applied a quasi-experimental design to investigate the relative effects of different factors likely to influence the profitability of illegal activities in different areas, and the same activities conducted outside protected areas. We chose hunting of wild herbivores for meat as a form of resource use known to yield considerably greater benefits when practised inside protected areas (Campbell & Hofer 1995; Hofer *et al.* 2000; Loibooki *et al.* 2002), and contrasted this with grazing and watering of cattle, which are activities unlikely to yield larger immediate benefits when conducted inside protected areas rather than outside such areas. We assumed that the likely benefits of illegal hunting would increase with increasing wild herbivore density and used natural fluctuations in wild herbivore density to test this assumption. We assumed that the value of forage and water resources to livestock owners would increase during periods of low precipitation (dry season), and that herds of livestock would be more easily detected by law enforcers than snares.

As a model of economic costs and benefits of illegal hunting in the Serengeti indicated that travel cost (calculated as the time taken to travel to and from a hunting site multiplied by the opportunity cost of travel) is more important in determining the spatial distribution of hunting activities than the cost of arrest based on penalties incurred if arrested (Hofer *et al.* 2000), our analysis is based on the expectation that travel costs increased with distance travelled, and that the chance of arrest was greater close to ranger posts than in areas without such posts (Campbell & Hofer 1995; Hofer *et al.* 2000). We selected study areas that varied with respect to both potential costs and benefits and predicted that use should occur where costs are perceived to be low, and where returns from exploitation are likely to outweigh cost.

Statistical analysis

Statistical analyses were performed using SYSTAT 10 (Wilkinson 2000). As data were not normally distributed, non-parametric tests were applied. For all tests $p < 0.05$ (two-tailed) was considered significant. Densities are presented as mean ± standard error (SE).

We used density of wild herbivores as one index of the potential benefit hunters might gain and the density of snares as an index of the effort exerted by hunters in an area. We used a post-hoc Kruskal-Wallis ANOVA test (Conover 1980) to compare predicted levels of hunting effort in different areas in relation to the cost of travel and cost of law enforcement. The areas considered were: Kirawira NP, Mihale NP, Mihale GR, Ndabaka NP and Ndabaka outside protected area. The unprotected area of the Mihale transect was excluded from this analysis, as no wild herbivores were observed in this area.

RESULTS

Livestock densities

In accordance with our predictions, no livestock were recorded along the Kirawira transect. The density of livestock within the protected area section (Serengeti NP and Grumeti GR) of both the Ndabaka and Mihale transects was lower (Ndabaka 2.8 ± 0.9 animals per km^2; Mihale 3.4 ± 1.4 animals per km^2) than the high density of livestock legally grazed outside the Serengeti NP on the Ndabaka transect (38.0 ± 4.1 animals per km^2; Wilcoxon Signed Rank $Z = -2.934$, $n = 11$, $p = 0.004$; Fig. 1*a*) and outside the Grumeti GR on the Mihale transect (35.3 ± 7.2 animals per km^2; $Z = -2.934$, $n = 11$, $p = 0.004$; Fig. 1*b*). These results indicate that herders knew the location of the Park and Reserve boundaries and mostly avoided taking their livestock into protected areas.

During the dry season, the density of livestock within the Serengeti NP and Grumeti GR along the Mihale transect was higher (7.52 ± 1.80 animals per km^2) than along the Serengeti NP section of the Ndabaka transect (0.68 ± 0.42 animals per km^2; Mann Whitney U = 3.0. $p = 0.007$, $n = 6$).

During the wet season, livestock was absent from the protected sections of the Mihale transect, but low densities of livestock were present in the Serengeti NP section of the Ndabaka transect (4.70 ± 1.22 animals per km^2), mostly between the Park boundary and the Mbalageti River.

Wildlife densities and illegal hunting effort

When the possible benefit to illegal hunters was scored in terms of wild herbivore densities, the Serengeti NP section of the Ndabaka transect was likely to yield the highest level of benefit (66.93 ± 17.06 animals per km^2). Moderate levels of benefit were likely from the Serengeti NP sections in the Kirawira and

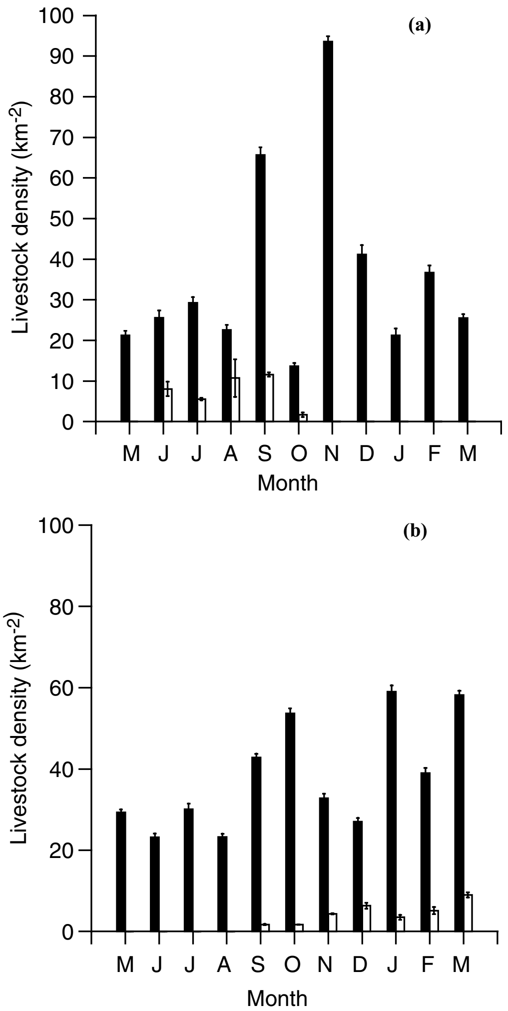

Figure 1 Mean monthly (May 2001–March 2002) livestock density per km^2 in (*a*) the Mihale transect, and (*b*) the Ndabaka transect. Solid bars = livestock outside the Serengeti NP and Grumeti GR; open bars = livestock inside the Serengeti NP and Grumeti GR.

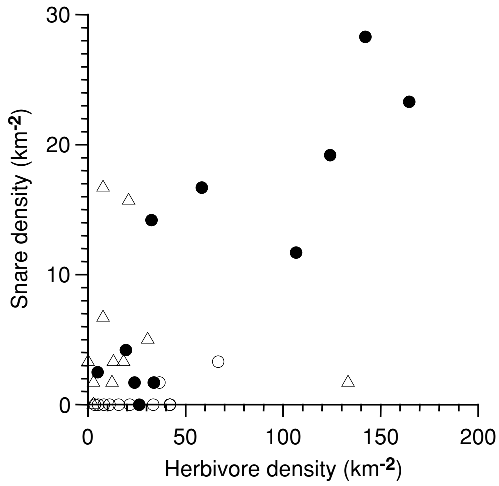

Figure 2 Plot of density of snares per km^2 against density of wild herbivores per km^2. (○) Serengeti NP section of the Mihale transect, (△) Grumeti GR section of the Mihale transect, (●) Serengeti NP section of the Ndabaka transect. Unprotected areas that contained few or no wild herbivores, and the Kirawira transect that contained no snares, not included.

Mihale transects respectively (31.20 ± 12.01 animals per km^2; 25.95 ± 5.99 animals per km^2), and the Grumeti GR section of the Mihale transect (22.65 ± 11.39 animals per km^2). Low levels of benefit were likely from the unprotected sections of the Ndabaka (2.77 ± 0.01 animals per km^2) and Mihale transects (no animals observed).

Combined data from the Serengeti NP sector of the Mihale and Ndabaka transect displayed the expected positive correlation between the mean monthly density of snares (hunting effort; Table 1) and the mean monthly density of herbivores (combined data from the Mihale and Ndabaka transects, Spearman Rank Correlation $r = 0.641$, $n = 22$, $p = 0.002$). The expected positive correlation between the mean monthly density of snares and the mean monthly density of herbivores was not found in the Grumeti GR section of the Mihale transect (Fig. 2; Spearman's $r = 0.20$, $n = 11$, not significant). Despite high densities of wild herbivores in Serengeti NP at Kirawira (Table 1, Fig. 3*a*), no evidence of illegal hunting (no snares, pitfall traps, or fences) was recorded along this transect. Owing to a very low density of wild herbivores outside protected areas (Fig. 3*b,c*), hunters could expect very poor returns and thus snares were rarely set in these areas.

Factors influencing illegal hunting effort

When areas were ranked according to their likely travel costs, and the hunting effort in these areas was predicted according to these ranks (Table 1), all pairwise comparisons of observed hunting effort between areas conformed to predictions, except for the comparison between the Serengeti NP section of Mihale and Kirawira, for which medium and low hunting efforts were predicted but equally low levels were observed in both areas (Table 1). These results indicate that travel is an important cost factor for hunters.

In contrast, when hunting effort was predicted on the basis of the likely chance of arrest (Table 1), then all pairwise comparisons of observed hunting effort between areas showed differences, however all differences except one were in the opposite direction to that expected. In particular, observed

Table 1 Observed and predicted hunting effort (snare density per km^2) based on travel costs and chance of arrest at the Kirawira, Ndabaka and Mihale transects (NP: National Park, GR: Game Reserve, unprotected: area outside both NP and GR). Results of post-hoc comparisons following Kruskal-Wallis test on observed hunting effort data; different letters indicate significant differences between sites, ? = unknown because hunting not observed.

Factor	*Ndabaka-unprotected*	*Mihale GR*	*Ndabaka NP*	*Mihale NP*	*Kirawira NP*
Observed hunting effort	0.00 ± 0.00	5.37 ± 1.70^a	11.23 ± 2.97^a	0.45 ± 0.23^b	0.00 ± 0.00^b
Travel cost	none	small	small	medium	high
Hunting effort predicted by travel cost	?	high	high	medium	low
Chance of arrest	none	small	medium	small	high
Hunting effort predicted by chance of arrest	?	high	medium	high	low

hunting effort in the Grumeti GR section of Mihale was significantly higher than in the NP section of this site when they were predicted to be equal, and, despite the presence of a guard post in the Serengeti NP sector of Ndabaka, the observed hunting effort was significantly higher than in the Serengeti NP sector of Mihale. These results indicate that the likely chance of arrest is perceived by hunters to be low and thus the potential costs associated with arrest do not have the expected influence on hunting effort. The only comparison that followed the expected direction was between the Serengeti NP section of Ndabaka and Kirawira (Table 1).

Seasonal changes in the densities of wild herbivores

Large fluctuations in the mean monthly densities of wild herbivores in each transect (Fig. 3) were caused by the migratory movements of wildebeest and zebra. High densities of wild herbivores were observed in Kirawira in June (Fig. 3*a*), in the Serengeti NP section of the Ndabaka transect between November and March (Fig. 3*b*), and in the Serengeti NP and Grumeti GR section of the Mihale transect in July, August, October, December and January (Fig. 3*c*). Neither resident nor migratory wild herbivores were present in the unprotected area outside the Grumeti GR along the Mihale transect (Fig. 3*c*) and were present only at very low densities in some months outside the Serengeti NP along the Ndabaka transect (Fig. 3*b*). This suggests that either the protected areas adequately encompassed the migratory routes or that migratory herds mostly avoided unprotected areas. Few resident herbivores persisted outside the protected areas, suggesting that populations of these species had been overharvested.

DISCUSSION

The results of this study are consistent with the idea that levels of illegal use of natural resources in the west of the Serengeti ecosystem were influenced by the likely value of the resources acquired and the probable costs associated with their acquisition.

Evidence of illegal hunting was found during the 11 months of this study along two of the three transects, suggesting that benefits of hunting mostly outweighed costs in these areas. Our results (Table 1) conformed to the expectation that level of illegal hunting decreased as the distance hunters travelled on foot to hunting areas increased. Travel cost is likely to be assessed not only in terms of distance travelled but also in terms of time that could be devoted to other activities (opportunity cost).

Illegal hunters mostly work at night by themselves or in small groups and use inconspicuous hunting methods. For this reason the likelihood of illegal hunting activities being detected is low, particularly in areas with dense vegetation and certain types of topography (Campbell & Hofer 1995). This may explain why high hunting effort occurred in the vicinity of the Ndabaka ranger post (Table 1, Fig. 3*b*). Our data are insufficient to test whether the absence of hunting effort at Kirawira was caused by the high chance of arrest afforded by two ranger posts and numerous tourist vehicles, a high travel cost to this area, or a combination of these factors. In general, the results of this study support optimality models developed for the Serengeti ecosystem that predicted that hunting would be depressed more by the cost of travel than the cost of arrest (Hofer *et al.* 1996; Hofer *et al.* 2000).

The relatively lower density of snares in the Serengeti NP section of the Mihale transect compared to that in the Grumeti GR section is most likely the result of a greater travel cost without increased returns, as herbivore densities in both areas were similar (Table 1).

The positive relationship between the density of snares and that of wild herbivores in the Serengeti NP sections of the Mihale and Ndabaka transects (Fig. 2) indicates that hunters increased their effort as the likely level of return increased. Our results cannot discern whether this was the consequence of a relatively stable number of hunters increasing their hunting effort as profitability increased, or was caused by an increase in the number of hunters setting snares in areas with high densities of herbivore, or both of these processes. The observed increase in the density of snares in areas containing high densities of herbivores was likely to be detrimental to wildlife, including non-target species (Hofer *et al.* 1993).

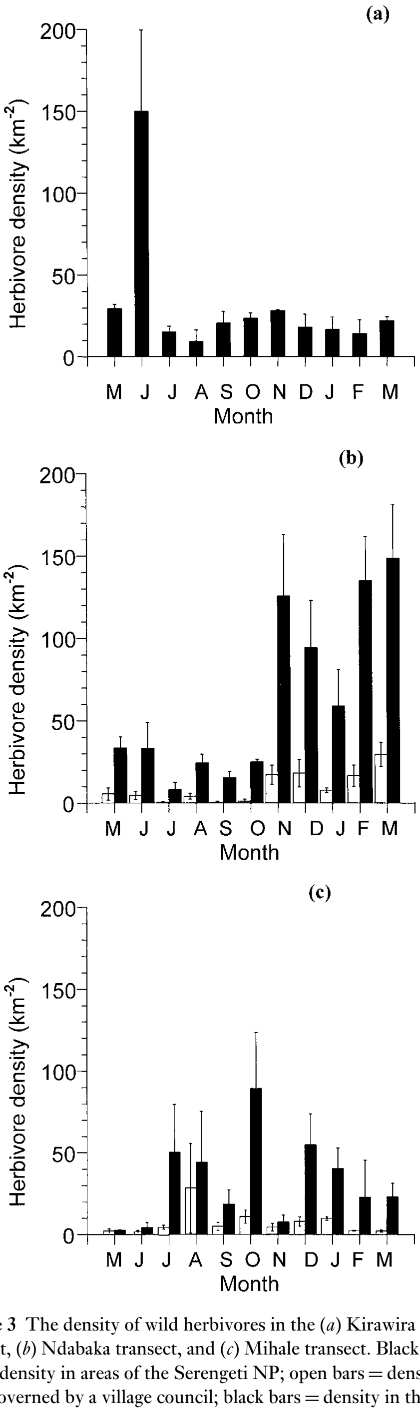

Figure 3 The density of wild herbivores in the (*a*) Kirawira transect, (*b*) Ndabaka transect, and (*c*) Mihale transect. Black bars = density in areas of the Serengeti NP; open bars = density in areas governed by a village council; black bars = density in the Grumeti GR. No wild herbivores were observed in the area governed by a village council in the Mihale transect between May 2001 and March 2002.

The highest densities of migratory herbivores recorded during the study occurred along the Ndabaka transect during the wet season (Fig. 3*b*). However, when herbivore densities along the Ndabaka transect were high, the density of snares in this area was lower than might have been expected, given the comparatively high snare density recorded in Grumeti GR section of the Mihale transect at far lower herbivore densities (Fig. 2). One possible explanation for this might be that travel by foot and the crossing of rivers in spate during the wet season are likely to be more costly than in the dry season, and drying illegally hunted meat for preservation and ease of transport is likely to be problematic during the wet season. Furthermore, during the wet season, villagers cultivate crops and, as Ndabaka was close to Lake Victoria, fishing may be more profitable than illegal hunting.

High densities of herbivores occurred in the Grumeti GR section of the Mihale site for a brief period of less than a month (Fig. 3*c*). The density of snares during this month was lower than that found in the Serengeti NP section of the Ndabaka site when similar densities of herbivores were present for several consecutive months (Fig. 2 and Fig. 3*b*). This indicates that hunters did not easily locate and immediately exploit large, transient herds of migratory herbivores that occupied an area for a brief period.

Overharvesting appears to have eliminated the wild herbivore populations in village managed areas outside the Grumeti GR at the Mihale site, and has decreased the wild herbivore population in village areas outside the Serengeti NP at the Ndabaka site.

During the dry season, the density of livestock within the Serengeti NP and Grumeti GR along the Mihale transect was higher than along the Serengeti NP section of the Ndabaka transect. This is probably because during the dry season the large river in the protected section of the Ndabaka transect (Mbalageti River) did not contain permanent water, and livestock owners moved their stock towards the shores of Lake Victoria where adequate forage and water were available during the dry season. Throughout the dry season the Grumeti River close to the Mihale transect did contain permanent water.

Despite high densities of livestock close to the boundary of the protected areas, domestic stock was rarely illegally present in these areas. This may indicate that livestock owners considered the chance of detection and likely financial penalties (fines or confiscation of livestock) too high in relation to the benefit gained from illegally acquired forage and the use of watering areas inside protected areas. As livestock owners are relatively wealthy members of local communities, they are likely to have less need to engage in illegal activities (Loibooki *et al.* 2001).

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Paper II

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Livestock loss caused by predators outside the Serengeti National Park, Tanzania

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ABSTRACT

Human–carnivore conflict is a serious management issue often causing opposition towards conservation efforts. In a survey of 481 households in seven different villages outside the Serengeti National Park in Tanzania, 67.4% of respondents owned livestock and 27.4% of all the households surveyed reported losses of a total of 4.5% of their livestock to wild predators over 12 months. This loss equated to an average annual financial loss of 19.2% (US $26.8) of their cash income. Livestock depredation was reported to be caused most often by spotted hyena (*Crocuta crocuta*) (97.7%), leopard (*Panthera pardus*) (1.6%), baboon (*Papio cynocephalus*) (0.4%), lion (*Panthera leo*) (0.1%) and lastly black-backed jackal (*Canis mesomelas*) (0.1%). Total reported losses during 2003 amounted to US $12,846 of which spotted hyena kills were reported to account for 98.2%. The mean annual livestock loss per household (of those that reported loss) was 5.3 head of stock, which represents more than two-thirds of the local average annual cash income. Depredation by large felids occurred only in a narrow zone along the protected area (<3 km), whereas spotted hyenas killed livestock even in households located far away (>30 km). Tolerance of livestock depredation among the respondents was low. Logistic regression models indicated that education improved tolerance, while for livestock owners higher depredation rates was linked to approval of lethal retaliation and effective protection measures was associated with a reduced desire of retaliation. We recommend that further research should identify the precise causes of livestock loss and which protection measures that can reduce depredation.

1. Introduction

Human population increase and technological development is rapidly reducing and fragmenting the available habitat for large carnivores. Although protected areas in principal are shielded from most human activities, the majority of African reserves are not large enough to maintain viable populations of these wide ranging species (Newmark, 1996; Woodroffe and Ginsberg, 1998). Non-protected and partially protected areas (i.e. IUCN categories < IV) therefore play a vital role in maintaining the existence of carnivores, both in order to increase population sizes and to allow greater genetic exchange between populations (Linnell et al., 2001; Treves and Karanth, 2003).

Large carnivores differ in their ability to adapt to anthropogenic landscapes. Behavioural plasticity and traits that give ecological flexibility and allow populations to recover rapidly from depletion have been identified as important factors for persisting close to humans (Cardillo et al., 2004). For example, in the Masai Mara National Reserve in Kenya, spotted hyenas

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(*Crocuta crocuta*) changed their daily activity rhythm, demographic structure, social behaviour and use of space as a response to increased disturbance from livestock grazing (Boydston et al., 2003). Small geographic range size, long gestation period, low species population density and high trophic level are all factors associated with high extinction risk in carnivores (Cardillo et al., 2004), but despite these biological traits, large carnivore survival ultimately depends on their conflict level 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). For instance, in the Koyiaki ranches outside the Masai Mara National Reserve, Ogutu et al. (2005) attributed substantially lower densities of lions (*Panthera leo*) outside the reserve in comparison to spotted hyenas, to less tolerance among Maasai pastoralists to lion depredation on livestock.

Lethal control has traditionally been the most common method for resolving conflicts between carnivores and livestock, leading to the eradication campaigns towards lions, spotted hyenas and African wild dogs (*Lycaon pictus*) in Southern Africa (Mills and Hofer, 1998; Rasmussen, 1999; Woodroffe and Frank, 2005). Some large carnivore species are therefore threatened after having experienced severe declines. For example, the African wild dog has been extirpated from 25 out of 39 former range countries, largely due to human persecution and habitat fragmentation (Fanshawe et al., 1997). According to the IUCN Red list, African wild dogs are listed as endangered, lions and cheetahs (*Acinonyx jubatus*) are listed as vulnerable, whereas spotted hyenas and leopards (*Panthera pardus*) are not categorised as threatened (i.e. lower risk and least concern respectively; IUCN, 2006). Although most large carnivores in Africa are by now legally protected, local people have few incentives to conserve them. Retaliatory killings of carnivores are common, since livestock depredation can have serious economic consequences for livestock keepers, and compensation schemes that may offset some of the costs are often lacking (Ogada et al., 2003; Frank et al., 2005; Graham et al., 2005). However, as examples from Europe and North America illustrate, compensation schemes do not provide an easy solution to the problem (Linnell et al., 1996; Treves and Karanth, 2003).

In Africa, Tanzania is one of the most important countries for large carnivore conservation (Nowell and Jackson, 1996; Mills and Hofer, 1998). Despite having an extensive protected area system, with several very large protected areas (>10,000 km^2), carnivore populations are still severely affected by human activity (Hofer et al., 1993, 1996; Packer et al., 2000). Moreover, human encroachment upon protected areas is intensifying the conflict between carnivores and livestock keepers. However, up to now most studies investigating livestock depredation in Africa have been conducted in areas with relatively low human density or immediately adjacent to protected areas (Rudnai, 1979; Mizutani, 1993; Karani et al., 1995; Butler, 2000; Ogada et al., 2003; Patterson et al., 2004; Kolowski and Holekamp, 2006). Few studies have investigated livestock depredation in areas with high human densities and how distance from the protected area influence livestock depredation. In this study, we explored through a questionnaire study the extent and impact of conflict between carnivores and agro-pastoralist outside the Serengeti National Park. Moreover, we quantify the perceived economic losses to local communities, and examine which factors influenced the approval of retaliatory killing as a carnivore depredation deterrent, since this is a common but illegal practice in Tanzania that has serious implications for carnivore persistence.

2. Methods

2.1. Study area

2.1.1. Climate and large mammals

The study was carried out on the north-western side of the Serengeti National Park (1°15′–3°30′ S, 34°–36° E, Fig. 1). The Serengeti National Park (14,763 km^2) is a World Heritage Site and the largest National Park in Tanzania. On the northern side it is buffered by several partially protected areas: Ikorongo Game Reserve (ca. 563 km^2), Grumeti Game Reserve (ca. 416 km^2) and the Ikoma Open Area (ca. 600 km^2). The average annual temperature in the study area is 21.7 °C, with an average annual precipitation of 800 mm in the east to 1050 mm in the north-western parts. The protected area network in the western Serengeti harbours large populations of resident ungulates including giraffe (*Giraffa camelopardis*), buffalo (*Syncerus caffer*), topi (*Damiliscus korrigum*), impala (*Aepyceros melampus*) and gazelles (*Gazella thomsoni* and *G. granti*), as well as large carnivores, such as spotted hyena, lion, leopard and cheetah (African wild dogs are currently absent from this area). The western corridor of the Serengeti National Park is characterised by the annual wildebeest (*Connochaetes taurinus*) migration, which in June–July travels through the partially protected areas on their way north (Sinclair, 1995). However, the partially protected areas only contain low numbers of resident wildlife, because of illegal bushmeat hunting, while the village areas contain almost no large wildlife (Rusch et al., 2005). In the partially protected areas all the larger carnivores are included in the trophy hunting quota, except cheetahs and African wild dogs.

2.1.2. People and livestock husbandry

In the agro-pastoral areas in the western Serengeti there is a high human population density (70 people/km^2), and a population growth rate of 2.5% in the period from 1988 to 2002 (human population in Mara Region in 2002 was 1.37 million) (URT, 2002). The villages are administrative units consisting of widely dispersed houses with no clear cut border to households belonging to other villages (Fig. 1), where the multiethnic villages consist of subsistence farmers who complement their livelihoods to varying degrees with livestock keeping and illegal bushmeat hunting. Generated income from these activities is partly used to pay taxes, village development contributions and levies, buy food and to purchase clothing (Loibooki et al., 2002; Holmern et al., 2004). The areas immediately adjoining the Serengeti National Park are experiencing a high pressure for scarce resources, and have a particularly high immigration rate (Campbell and Hofer, 1995).

In the western Serengeti, livestock husbandry is commonly practiced with mixed species herds of cattle, goats and sheep. A few farmers also keep donkeys and pigs. Livestock are usually taken out in the early morning (<09:00) and returned to night enclosures before sunset. Grazing

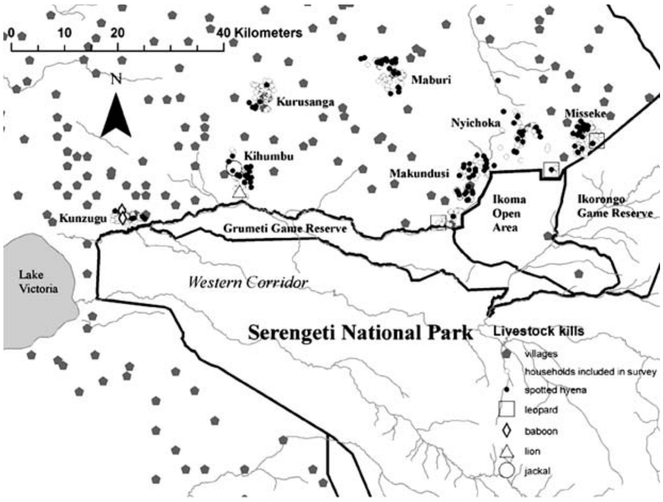

Fig. 1 – Distribution of reported livestock kills according to the predator responsible for the kill. The location of villages is shown as grey pentagrams, and the households from the seven villages included in the survey as open circles.

usually takes place close to the villages, but in the villages directly bordering the Ikorongo and Grumeti Game Reserves some illegal livestock grazing takes place inside the game reserves (especially in Grumeti Game Reserve). Livestock is always herded by people, in most cases by 1–3 adults, but sometimes also by children. At night cattle and donkeys are kept inside night enclosures (i.e. bomas), that are constructed by closely spaced vertical tree trunks. Goats and sheep are usually brought together in a separate small-stock hut that is constructed of poles and clay with grass roofing. Pigs are kept in separate pens constructed by poles and acacia bush (branches facing out). In addition, most households keep guard dogs. Extremely few people have access to firearms.

2.2. Data collection

The data were collected through a questionnaire survey between September and November 2004. Our survey encompassed 481 randomly chosen households from seven villages (based on household lists and including an equal proportion from each sub-village) in the western Serengeti, located at different distances from the closest protected area border; Kunzugu (3 km), Misseke (4 km), Kihumbu (5 km), Makundusi (8 km), Nyichoka (11 km), Kurusanga (20 km) Maburi (29 km) (see Fig. 1). The seven villages had, according to village records, a total of 2708 households, which means the survey canvassed 17.8% of the households. Interviews were conducted in Kiswahili by two Tanzanian scientists trained in interview techniques in the informant's home (the head of household or their wife), and the questionnaire included a mixture of fixed and open ended questions, which covered the respondent's background (age, tribe, education, etc.), livestock losses in the year 2003 and the approval of retaliatory killing of carnivores. Livestock losses were calculated against the size of herds in 2004. During interviews we used colour plates in field guides to help distinguish between carnivore species. Moreover, the respondents did not differentiate between striped hyena (*Hyaena hyaena*) and spotted hyena, but available data suggest that the much more common spotted hyena was the main predator on livestock in the area (Mills and Hofer, 1998). Likewise, black backed jackal (*Canis mesomelas*) is likely to be the jackal species present in the villages.

2.3. Statistical analysis

During the survey, we collected the GPS location of each household and the distance to the closest protected area border (i.e. game reserve or national park) was calculated by using ArcView 9.0 (Environmental Systems Research Institute, Redlands, CA, USA). We used logistic regression, to investigate which factors affected approval of retaliatory killing of carnivores. This was assessed by the statement: "Carnivores that cause damage to livestock are pests and should be shot". First we analysed the full data set, including both respondents with livestock and those without ($n = 411$), where we used the predictor variables: (1) distance to closest protected area (PA) border; (2) gender (male, female); (3) age (in years); (4) education (no education, primary school and secondary school pooled); and (5) livestock ownership. The interactions that were included were: education × PA distance, education × gender, education × age. Moreover, since the degree of dependency on livestock might influence the attitude against retaliatory killings, we regressed livestock numbers against crop area and saved these residuals (i.e. positive residuals less dependent on livestock). Thereafter, we ran an analysis for a subset of the data, including only livestock keepers ($n = 274$), where the residuals were used as a covariate in the model. In addition, this subset model included two more predictor variables: (1) perception of effectiveness of livestock measures; (2) number of livestock killed. All "don't know" answers on attitude were excluded from both analyses. We selected the most parsimonious models according to AIC_c

(Akaike Information Criterion corrected for small samples) (Burnham and Anderson, 2002). Moreover, we used Mann–Whitney *U*, Kruskal–Wallis one-way analysis of variance and χ^2 tests to investigate the occurrence of livestock depredation, where the considered significance value was $p < 0.05$. The analyses were done using SPSS 14.0 (SPSS, 2005) and R 2.3.0 Software (R Development Core Team, 2006).

3. Results

3.1. Livelihood and reported occurrence of large carnivores

Ninety-seven percent of the 481 respondents were agriculturalists. The primary source of income for respondents was subsistence farming (76.7%), followed by cash crop farming (21.0%), and other income generating activities (2.2%, i.e. sale of livestock products, gravel making). In addition to agriculture, respondents supplemented their income through livestock keeping (24.3%), trading (8.3%) and formal employment (4%).

In 2004, 67.4% of households ($n = 481$) kept a total of 13,029 livestock, with an average herd size of 27 head (±58.7 SD) of stock per household (Table 1). There was a substantial variation among households in the number of livestock owned (range: 0–547). Most livestock keeping households (55.5%) owned 50 or less animals, 11.9% owned more than 50 animals, whereas 32.6% did not own livestock. The majority of the herd was made up of cattle (63.8%) and goats (26%), while the rest were sheep, pigs and donkeys (Table 1). Most respondents reported that they kept their livestock in enclosures during the night (98.1%), while the rest left them tethered outside their house during the night. In addition, a total of 835 dogs were kept by 66.7% of the households in the study villages.

When the respondents were asked about the occurrence (in the past year) of large carnivores in close proximity to their village, all respondents in the survey claimed that spotted hyenas were present. In the villages located furthest away from the protected area (Maburi and Kurusanga) or in the far west (Kunzugu), very few respondents (0–4.2%) stated that large felids (lion and leopard) occurred nearby. In the villages

Table 1 – Mean composition of livestock herds per household in the study villages (2004)

Village	N	Cattle	Goats	Sheep	Donkey	Pigs	Mean[a]
Misseke	68	8.4	5.0	0.8	0	0.3	14.0
Nyichoka	56	17.7	8.1	1.4	0.02	0.5	27.1
Makundusi	68	30.4	12.1	4.9	0.2	0.03	53.3
Maburi	76	17.1	5.8	2.9	0.01	0	25.9
Kihumbu	69	28.5	9.6	5.2	0	0	43.2
Kurusanga	72	7.7	2.9	0.6	0.3	0	11.5
Kunzugu	72	6.8	6.5	2.8	0	0	16.1
Livestock per hh		17.3	7.1	2.7	0.08	0.1	27.1
% of the total herd		63.8	26.0	9.8	0.2	0.2	100

N, number of households (hh) sampled in the study villages.
Sixty-seven percent of households kept livestock; mean values estimated from all households, including those that had none.
a Mean number of livestock held by a household.

Table 2 – Economic valuation (US $) of reported livestock kills (n) by wild predators in the study villages in 2003

		Unit value (US$)	Spotted hyena	Leopard	Baboon	Lion	Jackal	Total (US$)
Cattle		60	5700 (95)	0	0	60 (1)	0	5760
Goats		11	4158 (378)	121 (11)	33 (3)	0	11 (1)	4323
Sheep		11	2343 (213)	0	0	0	0	2343
Donkey		120	120 (1)	0	0	0	0	120
Pigs		60	300 (5)	0	0	0	0	300
Total loss			12,621 (692)	121 (11)	33 (3)	60 (1)	11 (1)	12,846 (708)
Mean loss (±SD)								
	Per hh[a]		26.35 (70.63)	0.25 (3.51)	0.07 (1.12)	0.12	0.02	26.82 (81.99)
	Per hh[b]		96.03 (107.42)	0.92 (6.66)	0.25 (2.13)	0.45	0.08	97.73 (132.85)
Loss as a % of:								
	Herd		97.74	1.55	0.42	0.14	0.14	100
	Local per capita income[a]		18.82	0.18	0.05	0.09	0.01	19.15
	Local per capita income[b]		68.60	0.66	0.18	0.32	0.06	69.82
	Country per capita income[a]		8.23	0.08	0.02	0.04	0.01	8.38
	Country per capita income[b]		30.01	0.29	0.08	0.14	0.03	30.55

hh, household.
The conversion rate from Tanzanian shillings was 1 US $ = 1000 Tz.
a Considering all the respondents ($n = 481$).
b Considering only the respondents who reported loss ($n = 132$).

closest to the protected area (Misseke, Nyichoka, Makundusi, Kihumbu), 8.8–19.6% of respondents perceived that lions and leopards occurred, but Kihumbu deviated from this trend for lions where 68.1% of the respondents claimed they occurred close to their village. Only a single respondent reported cheetah to occur nearby (Nyichoka).

3.2. Livestock depredation

A total of 708 livestock were reported killed by predators in 2003 (Table 2). The majority of livestock killed were goats (55.5%), followed by sheep (30.1%), cattle (13.6%), pigs (0.7%) and donkeys (0.1%). Respondents attributed livestock depredation to be caused mainly by spotted hyena (97.7%), leopard (1.6%), baboon (0.4%), lion (0.1%) and lastly black-backed jackal (0.1%). In addition, a total of 171 dogs were reported lost to wild predators in 2003. Predation on dogs was perceived to be caused mainly by spotted hyenas (96.6%), jackal (1.1%) and some by unidentified predators (2.2%).

Most losses (74.8%) of livestock occurred during the night from the enclosures, while 25.2% occurred when the livestock were herded in the field during the day. Livestock losses due to spotted hyena did not differ significantly between wet and dry season ($\chi^2 = 0.004$, df = 1, $p = 0.953$), and predation by spotted hyena mainly happened at night ($\chi^2 = 93.2$, df = 1, $p < 0.001$). The same pattern was also apparent for dogs, where there was no difference between seasons ($\chi^2 = 1.1$, df = 1, $p = 0.312$), and significantly more dogs were killed during the night ($\chi^2 = 66.4$, df = 1, $p < 0.001$). Predation on dogs by spotted hyenas happened both when the guarding dogs were loose outside (66.2%), but also when they were kept inside the respondent's house (33.8%) during the night. For the other predators most attacks on livestock occurred during the day, except for one leopard and one lion attack which happened during the night.

There was no significant difference in distance to the closest protected area between households reporting loss and those that did not (M–W $U = 22155$, $z = -0.646$, $p = 0.518$). Depredation events caused by spotted hyena occurred in all the study villages (11.2 km ± 9.5, range: 0.6–31.3 km, $n = 132$), whereas for the other four predators depredation occurred only in households relatively close to the protected area (2.6 km ± 1.9, range: 0.7–6.3 km, $n = 7$), and this difference was significant (M–W $U = 124$, $z = -3.3$, $p = 0.001$). Percentage of reported livestock losses was significantly different between the villages (K–W $H = 32.2$, df = 6, $p < 0.001$). The greatest depredation rates occurred in Misseke (7.7%) and Nyichoka (7.6%), and the lowest in Kunzugu (1.6%). The perceived losses of livestock represented a total of 4.5% (±13.5%) of their livestock (considering all respondents) or 6.8% (±15.9%) when considering only livestock keepers. Mean annual livestock loss per household (of those that reported loss) was 5.3 head of stock (range: 1–33) or 16.6 % (±21.6%), which would cost two-thirds of their average annual income to restore.

3.3. Economic valuation of loss

The total economic loss of 708 livestock for the households included in the survey in the seven villages was US $12,846 for the year 2003 (Table 2). Spotted hyena contributed 98.2% of the economic value of livestock kills, while the economic impact of the other predators was low, although the consequences for the affected households may be serious. Despite being less numerously killed, cattle ($n = 96$) was the most important stock species in terms of economic value (44.8%, US $5760), because of its high value in comparison to goats and sheep. The annual mean economic loss to each household (all respondents) was estimated to be US $26.8 (19.2% of the local cash income). Average annual losses for those households that reported depredation ($n = 132$) was calculated to be US $97.7, which represented 69.8% of local income per household (Table 2).

Table 3 – Summary of logistic binomial regressions models of approval of retaliatory killing

Model	K	AIC_c	Δ_i	w_i
Full data set (n = 411)				
Education	2	472.5	0	0.075
Education + PA distance	3	472.7	0.16	0.069
Education + livestock owner	3	473.0	0.47	0.059
Education + PA distance + PA distance × education	4	473.3	0.81	0.050
Education + PA distance + livestock owner + gender + age+ PA distance × education + gender × education + age × education	9	480.5	7.98	0.001
Only livestock keepers (n = 274)				
Education + effectiveness of protection measures + number of livestock killed	4	303.9	0	0.050
Effectiveness of protection measures + number of livestock killed	3	304.1	0.13	0.047
Education + effectiveness of protection measures + number of livestock killed + PA distance	5	305.4	1.44	0.024
Education + effectiveness of protection measures + number of livestock killed + PA distance + livestock dependency	6	306.6	1.44	0.013
Education + effectiveness of protection measures + number of livestock killed + PA distance + livestock dependency + gender + age + PA distance × education + gender × education + age × education	11	314.9	6.09	<0.001

Model formulas are shown for the four most parsimonious and the global model, including the number of parameters (K, i.e. number of model terms plus 1 for intercept and error term), Akaike information criterion corrected for small samples (AIC_c), AIC_c differences ($\Delta_i = AIC_{ci} - AIC_{cmin}$) and Akaike weights ($w_i$, the model probabilities, i.e. normalized likelihoods of the models). The models are shown according to AIC_c, with the most parsimonious model at the top of the list.

3.4. Approval of retaliatory killing

Among the respondents a total of 73.4% approved the retaliatory killings of carnivores, 25.4% disagreed, and 1.2% did not know. The majority answered that carnivores should be killed as a response to livestock depredation, because they cause loss to farmers (54.9%), whereas the main reason for disagreeing was that carnivores are beneficial for the country (12.3%) (Table 5). Although for the full data set (including also people who did not own livestock, $n = 411$) the difference in AICc and evidence ratio did not clearly support any of the four top ranked models, the most parsimonious (i.e. with the lowest number of predictors) was the one containing only the variable education (Tables 3 and 4). Similarly, the most parsimonious model for the subset (including only people who owned livestock, $n = 274$) contained the variables, education, effectiveness of protection measures and number of livestock killed (Tables 3 and 4). Respondents with a formal education (primary or secondary school) were more tolerant of depredation, while both those experiencing a high loss of livestock and the respondents who perceived their livestock husbandry measures as not being effective were more likely to approve of retaliatory killing of carnivores.

Table 4 – Parameter estimates for the most parsimonious model of approval of retaliatory killing as judged by the AIC_c

Coefficients	Estimate	SE	z	p
Full data set (n = 411)				
(Intercept)	−0.83	0.13	−6.46	<0.001
Education	−0.68	0.26	−2.56	0.011
Only livestock keepers (n = 274)				
(Intercept)	−0.83	0.19	−4.17	<0.001
Education	−0.49	0.34	−1.45	0.148
Effectiveness of protection measures	−0.66	0.30	−2.19	0.028
Number of livestock killed	0.05	0.03	1.84	0.065

Table 5 – Comments given by respondents on reason for agreeing or disagreeing with the statement "Carnivores that cause damage to livestock are pests and should be shot" ($n = 171$)

Reason given for attitude	%
Negative responses (agree)	
Carnivores cause loss to farmers	54.9
Carnivores should be killed since no compensation for damage is paid	9.4
Carnivores are dangerous and may even attack people	4.7
Carnivores are not as important as other wildlife	1.2
Positive responses (disagree)	
Carnivores are beneficial to our nation	12.3
Wildlife has a right to live	7.0
Should just scare the carnivores away from the village area	5.8
Some carnivores are beneficial since they remove dead animals	2.3
Should report carnivore losses to wildlife officer	1.8
To kill wildlife would be against the idea of conservation	0.6

4. Discussion

Our results show that livestock depredation can extend relatively deep into non-protected areas depending on the prevalent predators, and can inflict serious economic losses to farmers. In the Serengeti National Park, the spotted hyena is the most numerous large carnivore and therefore it is not surprising that it is perceived to cause most of the livestock loss in our survey. In addition, the nocturnal and opportunistic foraging behaviour, together with the ability of spotted hyenas to take long-distance commuting trips, make them particularly adaptable to anthropogenic environments (Kruuk, 1972; Hofer and East, 1993; Mills and Hofer, 1998).

There are several potential weaknesses by relying solely on questionnaires that might have influenced our livestock loss data. Firstly, in Tanzania government taxes are levied partly on grounds of livestock numbers and although we made sure to identify ourselves as independent researchers during the study, we cannot rule out that the respondents deliberately underestimated their stock level because they were afraid that the results would somehow compromise them. Secondly, as Rasmussen (1999) pointed out, livestock holders may wrongly attribute stock that has died of natural causes to being caused by carnivores – through sheer neglect or prejudices towards specific carnivore species. Thirdly, livestock holders might have an interest in overestimating the rate of loss, because they might believe that it may be beneficial, either through benefits from compensation schemes or being targeted by outreach activities. However, in Tanzania farmers receive no form for compensation, and therefore have little incentive to misrepresent livestock losses. Outreach activities in the study area also do not focus on wildlife damages therefore farmers should have little to gain from overestimating loss. Lastly, respondents often bias their recollection of past events in favour of larger species, especially when sampling from multiple years (see Kruuk, 1980 for an example). We attempted to minimise this problem by only using the most recent year (2003), instead of using a longer time period. Despite these caveats, several studies show that livestock keeper's perception of livestock depredation gives a relatively reliable index of livestock depredation (Kruuk, 1980; Woodroffe et al., 2005). However, incorporating ways of verifying questionnaire data, either through use of wildlife officers that inspect kills or by providing an indirect measure through analysing scats, can be very valuable (Woodroffe et al., 2005; Wang and Macdonald, 2006).

Several studies show that low natural prey densities may be a strong contributor to high depredation rates (Meriggi and Lovari, 1996; Woodroffe et al., 2005; Kolowski and Holekamp, 2006). However, the relationship is not straightforward, since wolf (*Canis lupus*) predation on livestock may also be high where wolves have access to high natural prey densities (Treves et al., 2004). The low natural prey densities and high livestock densities around the Serengeti National Park may therefore contribute to the reported high depredation rates. On the Kenyan side of the Serengeti ecosystem Kolowski and Holekamp (2006) linked the arrival of the wildebeest migration to lower depredation rates on livestock. In contrast, we find no temporal variation in depredation rates, although the migration to some extent utilise the areas outside the Serengeti National Park. However, the migration travels quickly through the study area and does not venture into the villages far away from the protected area, and therefore seasonal fluctuations in prey availability are not likely to affect depredation rates.

At a regional scale livestock depredation is usually not considered a serious loss factor, and compared to other sources of loss (i.e. mismanagement, diseases, and theft) the impact of livestock depredation is usually relatively small. For example, across studies done in Africa, disease as a loss factor is 3-6 times larger in magnitude than livestock depredation (Mizutani, 1993; Karani et al., 1995; Rasmussen, 1999; Frank et al., 2005). Nevertheless, in some cases large carnivores can be a serious impediment for the economic situation of local livestock keepers (Mishra, 1997; Wang and Macdonald, 2006). Our data also emphasise that livestock depredation mainly by spotted hyenas is a severe economic constraint for households in the western Serengeti, where 27.4% of households ($n = 132$) in our survey of 481 households believed they had lost livestock to predators in 2003. The costs due to livestock loss were on average US $97.7 per household, which is almost one third of the GNI per capita in Tanzania (US $320 in 2004) (World Bank, 2006). However, local farmers in the study area have considerably lower income. Borge (2003) reported that in a survey covering 297 households from six villages in the western Serengeti the average annual cash income per household was US $140, which means that the stock loss constitutes two-thirds of the average annual income. Farmers also reported that carnivores sometimes killed several animals in one attack, which increases the cost to individual owners. However, in some cases farmers might be able to recoup some of the meat value of killed livestock by chasing off carnivores. The value of livestock (especially cattle) in pastoral and agro-pastoral society's has also a very important cultural aspect, which might contribute to their low tolerance of depredation compared to more commercially based enterprises (Patterson et al., 2004).

Large carnivores are also a common problem to human safety in Tanzania, and elsewhere (Løe and Røskaft, 2004; Packer et al., 2005). For example, in March 2004, a rabid spotted hyena was speared to death after attacking and badly mauling a woman in one of the study villages (Holmern, pers obs). Concerns for human safety combined with livestock loss may aggravate the situation and result in retaliatory killings, especially when funding, logistics and manpower constrain the response of wildlife management authorities. In the western Serengeti, there is widespread approval of retaliatory killing when carnivores kill livestock, or are perceived as a threat to human safety. Spotted hyenas are among the least liked large carnivore species in Africa and their dominance in our sample might have influenced the results. However, we cannot rule out that the precise wording of our statement might have contributed somewhat to increasing the approval rate, partly because it is a leading statement and it also contains two parts which can make interpretation of responses ambiguous. However, widespread support of retaliatory action in the western Serengeti was also reported by Kaltenborn et al. (2006), especially when spotted hyenas killed livestock. Likewise, Ogutu et al. (2005) reported that pastoral tribes in Kenya had a low tolerance of livestock depredation, while Ogada et al. (2003) found that retaliatory killings correlated with livestock loss rates. Our results also suggest that the number of livestock lost is associated with support of retaliatory killing. Considering the economic impact depredation can have on households, this is hardly surprising. Reducing the number of livestock lost to carnivores might contribute to less support of retaliatory killing, but even areas with comparatively low depredation rates can have a strong desire of lethal control (Linnell et al., 1996). Strong support of lethal wildlife management is by no means typical only for rural farmers in Africa, but has also been reported for North America (Kellert, 1985). However, identifying problem individual can be difficult, and lethal control of predators is only likely to cause a short-term respite from losses, because the same or other predator species rapidly re-establish themselves (Linnell et al., 1999; Stahl et al., 2001; Herfindal et al., 2005). But removal of problem carnivores, for example through trophy hunting in village areas, might facilitate public approval of protection for the remainder.

Developing ways of enabling farmers to benefit from the existence of protected areas could be a possible way forward (Wang and Macdonald, 2006). But in the case of the Serengeti National Park, benefits from outreach activities are currently grossly inadequate to offset costs associated with wildlife, and revenues from trophy hunting in the adjacent Game Reserves have a poor track record of reaching local farmers (Holmern et al., 2004). This situation seems also to be typical for other protected areas in Tanzania (Baldus and Cauldwell, 2004). Experience from community-based conservation projects show that distribution of benefits can be problematic and does not necessarily improve conservation (Newmark and Hough, 2000; Johannesen and Skonhoft, 2005). However, implementing incentive schemes aimed at conserving endangered carnivores can work, as encouraging results reported by Mishra et al. (2003) for snow leopard (*Uncia uncia*) show. This is further supported by Johannesen (2006) that demonstrate through modelling that it is crucial for such programs to forge a link between benefit levels and conservation friendly behaviour in order to improve wildlife conservation and human welfare.

Compared to other studies in Africa, the livestock loss reported in this study is among the highest recorded and needs to be addressed, both because it is an economic constraint to households, but also because it increases the likelihood of approving of illegal retaliatory killings, which may be of serious concern for the conservation of endangered carnivores (Rudnai, 1979; Kruuk, 1980; Mizutani, 1993; Karani et al., 1995; Rasmussen, 1999; Butler, 2000; Frank et al., 2005; Kolowski and Holekamp, 2006). Our results point out the need of formal education in order to improve attitudes, which is in accordance with many similar studies (Lindsey et al., 2005; Woodroffe et al., 2005). Prejudice against carnivores and misconceptions of the actual causes of loss are quiet common among farmers (Rasmussen, 1999). The development of better education in the region, particularly the establishment of more primary and secondary schools which at the moment have a poor coverage, along with education programmes on wildlife conservation might lead to increasing tolerance and decreasing misconceptions. Earlier research in Africa and Asia has also identified the need of improving livestock husbandry to reduce conflict levels (Kruuk, 1980; Mishra, 1997; Rasmussen, 1999; Ogada et al., 2003). It is therefore essential that further research should address the precise role of livestock husbandry practices in explaining depredation events outside the Serengeti National Park. The construction of night time enclosures might therefore be of particular importance, since most depredation occurs after dark.

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Paper III

Disease is a major cause of livestock loss in villages surrounding western Serengeti, Tanzania

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Abstract

Diseases have been responsible for high livestock losses in sub-Saharan Africa, delaying the introduction of cattle-based economies for many years. In this study, we quantified and compared the magnitude of livestock losses per household due to diseases, theft, depredation, and poor management in the grazing field from April to December 2006 in villages located in the western Serengeti. Furthermore, we compared such losses in villages situated close to or farther away from Serengeti National Park. Diseases were responsible for higher livestock losses than other loss causes. Overall, diseases were responsible for 3.5 – 7.0% livestock loss per household during the period of nine months, costing them US$ 83.5. This loss is equivalent to 59.6% of the average annual household income. The cost per household of theft and poor management in the grazing field was US $ 3.0 and US $ 11.4, respectively. The cost of depredation recorded was higher in the household located far away from the park boundary. The depredation cost per household in the four villages was US$ 16.5. Spotted hyena *Crocuta crocuta* was the only reported predator killing livestock and it killed more sheep and goats than cattle. We recommend better education on animal husbandry practices and extension service to help in maintenance of livestock health and to prevent theft and loss while grazing. To reduce livestock depredation, we suggest that night enclosures for livestock should be improved, especially in villages that are situated further away from national parks.

Introduction

In sub-Saharan African, diseases have been documented to be responsible for high losses in livestock production (Gifford-Gonzalez, 2000). Historically, diseases have been an important factor that delayed the introduction of cattle-based economies by as much as a thousand years after the first appearance of small stock in both eastern and southern Africa (Gifford-Gonzalez, 2000). Diseases that are often fatal to livestock production, especially for cattle in sub-Saharan, Africa include wildebeest-derived Malignant Catarrhal Fever (MCF), East Coast Fever (ECF), Foot and Mouth Diseases (FMD), worms (helminthes), Rift Valley Fever (RVF), rinderpest, anthrax as well as trypanosomiasis (Rwambo et al., 1999; Thomson et al., 2003; Kock, 2003). Livestock diseases have economic consequences on livestock husbandry at two levels; 1) at the domestic level, the diseases are responsible for direct loss due to mortality or indirectly through lowered production and/or the cost of treatment and prevention (Perry et al. 2002; Kock, 2003). 2) At the international level, diseases may affect any opportunity for export of livestock and livestock products between regions or continents, jeopardizing the exchange of products for foreign currency (OIE, 2003; Kock, 2003). Because of negative attitudes of livestock keepers towards wild carnivores, they often claim wild carnivores being responsible for higher losses of livestock despite the direct and indirect impacts of livestock diseases (Mwangi, 1997; Rasmussen, 1999). However, several factors may equally cause significant livestock loss, for example theft, drought and poor livestock husbandry (Ogada et al., 2003). The high prices received for livestock in the livestock auctions, make the theft of animals a lucrative business. In Africa theft may increase with the number of animals the household own, because it may be difficult to notice a loss of one or few animals in a group of several hundred individuals. Moreover, livestock theft may vary depending on the season or between years. During the rain season, it may be easy to follow the tracks the animal stolen has left behind to the destination. Thus, thieves would avoid this season. The night with a full moon is not conducive for livestock raiders because it is possible for livestock keepers to see the livestock in the night holding enclosure from within the household living quarters. Elsewhere outside Africa, livestock theft has been considered the most significant rural crime (WASDA, 2007). Drought may affect livestock directly by reducing the available food and water; hence animals may be so weak that they easily succumb to diseases. Indirectly drought normally associates with famine which drive the livestock keepers to sale some individuals to buy food.

The level of livestock depredation may be intentionally exaggerated to attract public attention and/or to mask effects of poor livestock management (Nabane, 1995; 1996; Infield, 1996). Such negative attitudes towards carnivores due to perceived levels of predation have been cited as a challenging issue in both wildlife conservation and rural development (Woodroffe et al., 2000). In different parts of the world, conflicts between human and wild carnivores have been well documented (e.g. Treves and Karath, 2003; Treves et al., 2004; Røskaft et al., 2007). This conflict has resulted in direct persecution of carnivores to get rid of them close to human settlements (e.g. Mill and Hofer, 1998; Woodroffe and

Frank, 2005), and resulted a general dislike of such animals. For example, American citizens do not like wolves *Canis lupus* and coyotes *C. latrans* (Kellert, 1985). Likewise, sheep farmers in Norway show negative attitudes towards bears *Ursus arctos*, wolves and lynx *Lynx lynx* (Kaltenborn et al., 1998; Vittersø et al., 1998; Kaltenborn et al., 1999; Røskaft et al., 2007). In some parts of Africa, the same negative attitudes towards carnivores have been reported as well (Lindsey, et al 2005; Kalternborn et al., 2006; Holmern et al., 2007). For example, livestock keepers in Africa have been reported to kill and poison carnivores to reduce the perceived conflict over livestock depredation (Stuart et al., 1985; Berry, 1990; Holekamp and Smale, 1992).

The aim of this study was to record and discuss factors responsible for livestock loss in households from the villages surrounding the western Serengeti. The livestock loss causes that were recorded in each selected household included diseases, theft, depredation and loss in the grazing field. We recorded number of animals slaughtered for meat, sold and/or bought as well as newborn calves.

Methods

Study area

Serengeti National Park (SNP) is situated west of the Rift Valley and the western border is close to Lake Victoria while the northern edge borders Kenya (Fig. 1). The central part of the current park was designated as a Game Reserve in 1929. In 1940 hunting was banned and in 1951 it was declared a national park. In the time following, the borders have been modified as the park has expanded. In 1981 Serengeti was inscribed as a World Heritage Site. The park covers 14 763 km^2 and is the core of the Serengeti ecosystem that includes Ngorongoro Conservation Area, Maswa Game Reserve, Ikorongo-Grumeti Game Reserves and Loliondo Game Controlled Area, in Tanzania as well as the Maasai Mara Natural Reserve to the north in Kenya.

The current study was conducted in the villages surrounding western Serengeti (Fig. 1), one of the areas of the SNP that currently suffers from conflict between conservation priorities of the park and priorities of local communities (Hofer et al., 1996; Loibooki, 1997). This is a section of the Serengeti ecosystem that extends westward to Lake Victoria with a relatively high human population density (i.e. 70 people/km^2; growing at a rate of 2.5% between 1988 and 2002, URT 2002). The majority of local communities along the boundaries of the western Serengeti are subsistence farmers who keep livestock and practice crop production. Many of the farmers obtain natural resources inside the protected areas for home consumption. For instance, during the dry season, livestock keepers illegally graze and water their livestock in the protected areas (Nyahongo et al., 2006). In addition, illegal hunting within the protected areas is well documented (Arcese et al., 1995; Campbell and Hofer, 1995; Loibooki et al., 2002; Nyahongo et al., 2006). The illegal bushmeat hunters may sell the illegally obtained meat to generate income (Arcese et al., 1995; Hofer et al., 1996; Loibooki, 1997).

Data collection

The current study was conducted between April and December 2006. Households were selected in the following villages: Robanda, Nyamakendo, Nattambiso and Kowak. The first three villages were within 10 km from the boundary of the park while Kowak village was located about 80 km from the park. Household were selected randomly according to household lists in the villages. For practical reason (livestock counting time), we omitted household with more than 200 individual cattle, goats or sheep. The first three months (January, February and March) were spent in villages to introduce researchers to livestock keepers and to establish baseline data on livestock numbers per selected household. Livestock owners were informed about the essence of this study and was assured that the data was only collected for research purpose and not for other purposes like baseline data for setting livestock levees by the government. After establishing the baseline data (i.e. initial numbers of livestock per selected household), we appointed enumerators from the respective villages that consists of livestock owners enumerating any livestock that suffered loss (death due to diseases, loss while grazing, theft, predation), own consumption (slaughtering) or gain (new-born, bought or paid as dowry). While enumerators were collecting data on a daily bases, the researcher visited each household after every three months to recount the animals again in order to cross check the data that enumerators collected. Furthermore, livestock owners were asked about the livestock status during the period of the past three months. Livestock were either counted in the morning before being sent out for grazing in the field (normally 2 to 3 km away from the night holding enclosures) or in the evening when they were brought back to the night holding enclosures (the counting rate was 15 to 20 households per day and we spent one week in each village).

All livestock were prized according to matured livestock because market prices for livestock are only set for mature animals. This allowed us to be able to calculate the mean cost of livestock loss causes per household per year.

Statistical analyses

All analyses were performed using SPSS 14 statistical package (SPSS, 2005). Descriptive statistics were used to calculate means and standard deviation while non-parametric tests were applied to test the differenced among the loss factors, household and livestock species. The mean number of livestock was the average of the livestock count each three months. The proportions (%) of livestock loss/gain causes or household expenditure were calculated as the ratio of each variable to the calculated mean livestock numbers. For all tests $p < 0.05$ was considered significant.

Results

Livestock gain and loss causes

Mean household livestock population variation and the subsequent cost or benefits when presented in monetary term for the current values of livestock species in each village are summarized in Table 1 and Table 2.

Regardless of household locality, various loss causes affected livestock differently (cattle: Friedman test, $\chi^2 = 233.72$, df = 3, n = 182, p < 0.001; goats: Friedman test, $\chi^2 = 134.07$, df = 3, n = 155, p < 0.001; sheep: Friedman test, $\chi^2 = 81.26$, df = 3, n = 123, p < 0.001). Furthermore, the mean number of cattle and goats sold per household was higher than the number slaughtered (cattle: Wilcoxon sign rank test, Z = -7.24, n = 182, p < 0.001; goats: Wilcoxon sign rank test, Z = -3.214, n = 155, p = 0.001) but this was not the case for sheep (Wilcoxon sign rank test, Z = -0.70, n = 123, p = 0.484). In all households, new born calves, and not animals bought or paid as dowry, was the significant source of replenishment of livestock numbers (cattle: Wilcoxon sign rank test, Z = -8.54, n = 182, p < 0.001; goats: Wilcoxon sign rank test, Z = -8.38, n = 155, p < 0.001; Sheep: Wilcoxon sign rank test, Z = -7.56, n = 123, p < 0.001).

Comparison of livestock loss causes among villages

The mean number of goats and sheep that was depredated was higher in Kowak than in villages that were closer to the park boundary although this was not significant statistically (Table 1). In all livestock depredation events spotted hyena *Crocuta crocuta* was the only carnivore reported to be responsible for livestock killing.

Mean number of cattle that died of diseases differed significantly among the villages (Kruskal-Wallis, H = 17.072, df = 3, p = 0.001). Furthermore, the difference in mean number of cattle that were stolen among villages was almost significant (Kruskal-Wallis, H = 7.124, df = 3, p = 0.068). The remaining cattle loss causes did not differ significantly among villages (p > 0.09 for all cases).

Likewise, the effect of all loss causes in goats did not differ significantly among the four villages (p > 0.076 for all cases). However, for sheep, losses due to diseases and poor management differed significantly among the villages (Kruskal-Wallis, H = 9.10, df = 3, p = 0.028 and H = 8.85, df = 3, p = 0.031, respectively), while theft and depredation on livestock had similar effect among the villages (p > 0.118 for all cases).

Comparison of livestock loss causes among livestock species

Generally, regardless of distance from the park boundary, mean number of livestock species that were sold, slaughtered for food and that were killed by spotted hyenas differed significantly between livestock species (sold: Kruskal-Wallis, H = 10.82, df = 2, p = 0.005; slaughtered: Kruskal-Wallis, H = 17.09, df = 2, p < 0.001; predation: Kruskal-Wallis, H = 14.01, df = 2, p = 0.001). Households sold more cattle (mean rank = 248.5) than goats (mean rank = 231.4) or sheep (mean rank = 202.7). However, households slaughtered more goats for food (mean rank = 249.6) than sheep (mean rank = 243.2) or cattle (mean rank = 205.6). In contrast, sheep were more frequently killed by spotted hyenas (mean rank = 246.6) than goats or cattle (goat: mean rank = 241.1; cattle: mean rank = 210.6). The remaining loss causes did not differ significantly among species ($p > 0.151$).

Economic significance of livestock loss or gain causes

In total, the mean value of livestock that household from four villages own was US$ 2121 (sum of mean cattle, goats and sheep per household) and newborn calves per household worth US$ 202.7. When the effect of livestock loss causes were pooled, disease were responsible for US$ 83 (sum of mean losses in cattle, goats and sheep) per household, while wild carnivores caused only US$ 12.6 per household (15.2% of loss due to diseases). On average, the value of livestock sold per household was US$ 57.8. This was 30.4% less than the value the household lost due to diseases. Livestock losses due to theft and poor management were US$ 14.4 while animals slaughtered for meat worth US$ 16.5 per household. Each village cost-benefit analysis of each loss or gain causes is summarized in Table 2.

Discussion

The results of this study suggest that diseases are responsible for higher livestock loss than any other livestock loss causes within and among villages. However, for sheep losses due to diseases and poor management differed significantly among the villages. Mean number of cattle and goats sold per household was higher than the number slaughtered in all villages. In each household, new born calves were the significant source of replenishment of livestock numbers. Mean number of livestock species that were sold, slaughtered for food and that killed by spotted hyenas differed significantly between livestock species whereby goats and sheep were more slaughtered for food than cattle.

Disease is the major factor responsible for higher livestock losses in sub-Saharan Africa (Gifford-Gonzalez, 2000). This factor alone, although not realized by farmers in Africa (Mwangi, 1997), was responsible for a loss of US$ 83.5 per household during the nine months study period (Table 2). When this figures was compared to average annual cash income per household in the western Serengeti (US$ 140, Borge, 2003), diseases were responsible for 59.6% of average annual household income in the target villages. On average, diseases contributed to 5.1 times higher in livestock losses than depredation cost. This observation is consistent with previous studies in the same area when the farmers were requested to rank the major factors that were responsible for higher livestock losses (Nyahongo, 2004). Livestock keepers may not observe the direct effect of diseases to their livestock production due to the fact that the sick animals may be slaughtered and used as food or sold to neighbors while carnivores often consume all edible parts of a kill; leaving nothing for human consumption. Moreover, diseases often kill larger number of new born calves than adults (personal observation, 2006). Livestock keepers may not observe this as an important loss because the capital investment in terms of veterinary service, feeding or grazing time and/or output in terms of meat or money (when sold) is relatively much lower for new-born calves than for adults. Moreover, due to poor livestock management records, livestock keepers may not be able to know how many livestock they loose to diseases within a specific period of time. Most of household we visited did not have any record showing number of livestock, new born or even the last time the animal was treated and the cost implication. In contrast, when a predator breaks in the livestock enclosures, usually at night (Nyahongo, 2004; Kolowski and Holekamp, 2006; Holmern et al., 2007), it may kill several adult animals and this may result in serious economic consequences for livestock keepers. However, since the compensation scheme that may offset some of the costs are always lacking in Tanzania, negative attitudes towards carnivores may have developed among farmers, which have resulted in retaliatory killing practices of carnivores in or close to village proximities (Holekamp and Smale, 1992; Ogada et al., 2003; Dickman, 2005; Frank et al., 2005; Graham et al., 2005; Holmern et al., 2007).

Sheep and goat depredation by spotted hyena was higher though not statistically significant, in the village that was located far away from the park boundary. This suggest that even in open areas with high anthropogenic activities, still there are some refuges for some large carnivores like spotted hyenas. This observation suggest a change in wildlife policies that insist management of wildlife only in the established protected areas such as national park, game reserves and game controlled areas. It would be of the conservation interest and for the future conservation if wildlife management policies include all wild animals in the protected areas as well as in anthropogenic dominated areas. Certain carnivore species such as spotted hyenas have the ability to commute up to 80 km (Hofer and East, 1993) allowing them to forage even in villages located farther from the protected areas. The findings of the present study gives an alternative idea that is inconsistent to the idea that high depredation are only highest closest to the reserves boundary (Mwangi, 1997). However, as Woodroffe (2000) puts it, behavioral plasticity of certain carnivore species facilitate their adaptive adjustment to an increasingly precarious lifestyle in proximity to human, a fact that was reported for spotted hyena of Maasai Mara ecosystem (Boydston et al., 2003). However, it is difficult to establish that the spotted hyena reported in the distant villages commuted from Serengeti or were resident to the village areas.

Analyses of our data suggest that cattle are kept for solving household needs that require relatively huge amount of money while goat and sheep are kept to tackle small household needs and/or slaughtered to provide meat protein to the household. This might be due to the fact that the economic value of one cattle is equivalent to about four goats or sheep. These ideas are supported by comparing the number of cattle, goats and sheep that were slaughtered and those that were sold. The proportions of cattle slaughtered were far less than those sold by households in the study villages (Table 1, Fig 2).

Variables like available water and grazing land, weather, market prices of meat (that could lead to elevated theft rate), animal population dynamics in the villages and in the protected areas adjacent to village areas, diseases occurrence may, as the variables included in the analyses, show considerable between year variations. These confounding variables, which cannot be controlled for in a snap shot study like the present one, might have influenced the data we collected. For instance, death of livestock due to diseases may increase with drought or with rain intensity and duration, which cannot be precisely compared within a year because intensity of rain and duration of rain seasons may differ in different areas each year in Tanzania affecting pasture quality and available water for animals. Drought may also influence the number of livestock sold to buy food, because crop production in the country largely depends on rain. Weather, on the other hand may influence the survival of new born calves or may influence the level of depredation. Woodroffe and Frank (2005) observed that rate of livestock depredation by large carnivores increase with the increase in rainfall. Exclusion of households with very many animals might have further led to underestimation of livestock loss because more death from disease (due to density dependent danger of infectious diseases), livestock depredation, theft and loss due to poor management in the grazing field may be expected to increase with increase in livestock numbers.

Concluding remarks

The results from this study showed that diseases are the major cause of livestock loss in the villages and that the levels of loss do not vary much among the households in the western Serengeti. In contrast, livestock depredation by spotted hyena was relatively low, although it was relatively higher for goats and sheep in the households from the distant village. Likewise, poor management and theft that can be managed at household level causes livestock losses as well. However, at the household level, a single depredation event may cause a serious economic loss.

Livestock depredation may be higher in the areas with high human activities, which encourage wildlife managers, conservationists and wildlife ecologists to think deeply about livestock depredation along the gradient of distance from the park and the future conservation of the carnivores along the same gradient.

This study suggest that local people would benefit from better education on animal husbandry practices and extension service to help them maintain the health of their livestock and to prevent theft and loss of livestock while grazing. We recommend that diseases control and management should be integral part of regional and national development programs to limit disease transmission between livestock and wildlife and even among livestock in the villages. Further studies on the types and epidemiology of diseases causing major livestock losses in the area should be conducted in order to design appropriate diseases control measures.

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Biographical sketches

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Table 1. Mean number of livestock per household and proportion of livestock loss or gain causes (livestock loss causes: diseases, loss in the bush (poor management while grazing), depredation and theft; livestock gain: newborn and bought/paid as dowry; household expenditure: sold and slaughtered for meat)

Livestock numbers and loss/gain	Robanda			Nyamakendo			Nattambiso			Kowak			Overall		
	Cattle	Goats	Sheep	Cattle	Goats	Sheep	Cattle	Goats	Sheep	Cattle	Goats	Sheep	Cattle	Goats	Sheep
Mean numbers	23.4	9.4	13.0	15.2	13.9	8.3	21.6	16.8	14.6	22.5	8.5	9.0	20.5	12.1	11.2
(± SD)	(17.2)	(6.0)	(22.9)	(12.9)	(12.2)	(14.0)	(12.2)	(15.0)	(14.7)	(22.1)	(11.7)	(11.8)	(16.8)	(11.2)	(15.8)
Livestock gain (%)															
Newborn	10.3	21.3	16.2	5.9	15.1	10.8	9.3	16.1	18.5	5.3	11.8	11.1	7.7	16.1	14.2
Bought	1.7	1.1	0.8	3.3	3.6	1.2	2.3	2.4	2.0	0.9	2.3	2.2	2.1	2.4	1.6
Livestock loss (%)															
Diseases	3.4	4.3	5.4	2.6	6.5	2.4	5.1	10.1	5.5	3.1	7.1	6.7	3.5	7.0	5.0
Loss in the bush	0.4	0	1.5	0.2	1.4	0	0.5	1.2	1.4	0.4	1.2	1.1	0.4	0.9	1.0
Depredation (%)	0.4	0.3	1.5	0.1	0.7	1.2	0.1	1.8	0.7	0.3	4.7	5.6	0.2	1.9	2.2
Theft	0	0	0.1	0.2	0.1	1.2	0.1	0.1	0.1	0.2	0.3	0.3	0.1	0.1	0.4
Household expenditure (%)															
Sold	2.1	3.2	4.6	4.6	5.8	2.4	2.8	2.4	1.4	1.3	3.5	4.4	2.7	3.7	3.2
Slaughtered	0.4	1.1	0.8	0.5	1.4	1.2	0.5	3.0	2.0	0.1	2.3	2.2	0.4	2.0	1.6
Mean recruitment (%)	5.3	13.5	3.1	1.0	2.8	3.6	2.5	-0.1	9.4	0.8	-5.0	-7.0	2.4	2.8	2.3

Note: Sample sizes: Robanda (n = 37 households for cattle, n = 10 for goats and n = 15 for sheep); Nyamakendo (n = 49 households for cattle, n = 49 for goats and n = 26 for sheep); Nattambiso (n = 46 households for cattle, n = 45 for goats and n = 28 for sheep); Kowak (n = 50 households for cattle, n = 51 for goats and n = 54 for sheep).

Table 2: Cost and benefit implications of livestock loss and/or gain causes (US $)

Livestock numbers and loss/gain	Robanda			Nyamakendo			Nattambiso			Kowak			Overall values (US$)		
	Cattle	Goats	Sheep	Cattle	Goats	Sheep	Cattle	Goats	Sheep	Cattle	Goats	Sheep	Cattle	Goats	Sheep
Mean value of livestock	1872.0	188.0	260.0	1216.0	278.0	166.0	1728.0	336.0	292.0	1800.0	170.0	180.0	1654.0	243.0	224.0
Livestock gain values (US$)															
Newborn	192.8	40.0	42.1	71.7	42.0	17.9	160.7	54.1	54.0	95.4	20.1	20.0	130.1	39.1	33.5
Bought	31.8	2.1	2.1	40.1	10.0	2.0	39.7	33.9	5.8	16.2	3.9	4.0	31.9	12.5	3.5
Livestock loss (US$)															
Disease	63.6	8.1	14.0	31.6	18.1	4.0	88.1	10.1	16.1	55.8	12.1	12.1	59.8	12.1	11.6
Depredation	7.5	0.6	3.9	1.2	1.9	2.0	1.7	6.0	2.0	5.4	8.0	10.1	4.0	4.1	4.5
Loss in the bush	7.5	0	3.9	2.4	3.9	0	8.6	4.0	4.1	7.2	2.0	2.0	6.4	2.5	2.5
Theft	0	0	0.3	2.4	0.3	2.0	1.7	0.3	0.3	3.6	0.5	0.5	1.9	0.3	0.8
Household expenditure (US$)															
Sold	39.3	6.0	12.0	55.9	16.1	4.0	48.4	8.1	4.1	23.4	5.9	7.9	41.8	9.0	7.0
Slaughtered	7.5	6.0	2.1	6.1	3.9	2.0	8.6	10.1	5.8	1.8	3.9	4.0	6.0	6.0	4.5

Note: Mean local market price of one cattle in the study area was US$ 80, and for goat/sheep was US$ 20 in 2006, (the prices were for mature animals).

Figure legends:

Figure 1. Map of the western Serengeti showing the sampled villages.

Figure 2. Overall livestock population dynamics (loss and gain) in four villages recorded from April to December 2006.

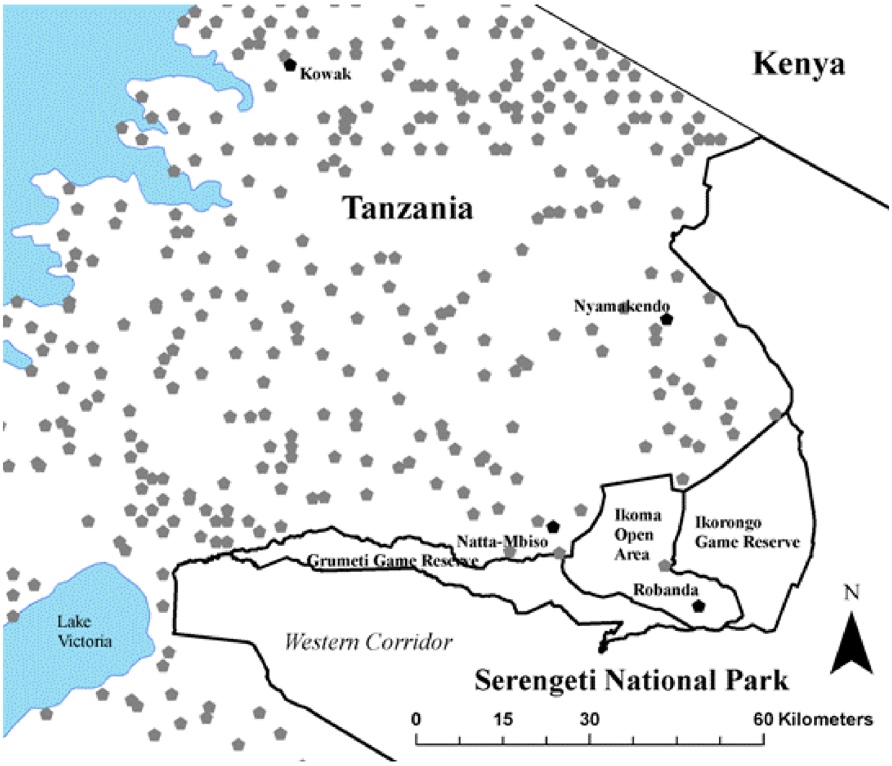
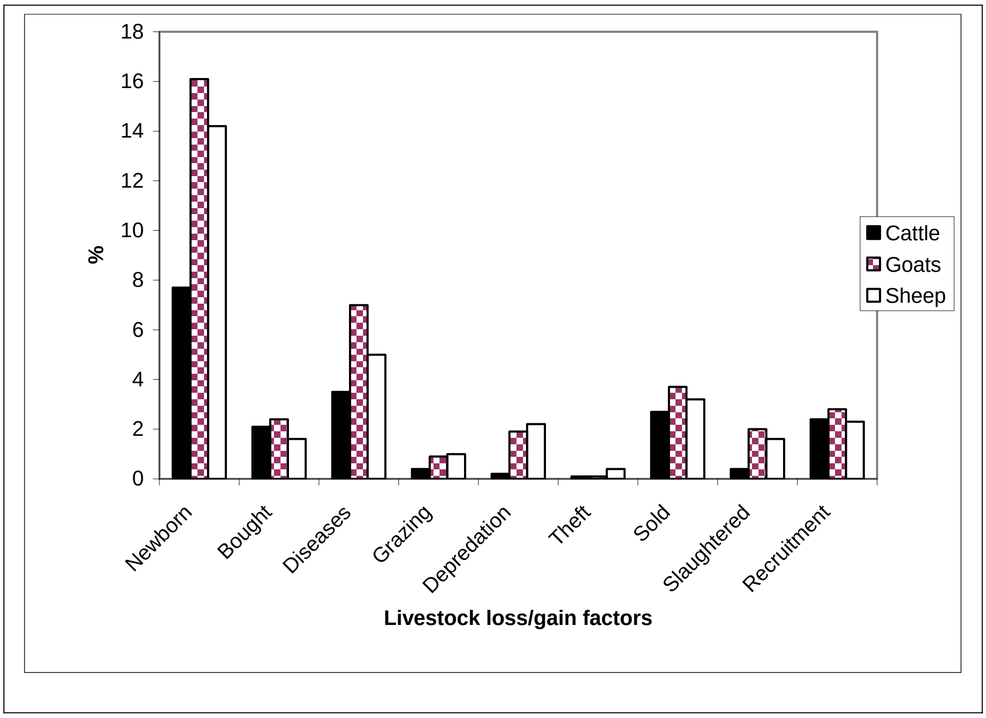

Kenya
Kowak
Tanzania
Nyamakendo
Natta-Mbiso
Ikoma
Open
Area
Ikorongo
Game Reserve
Grumeti Game Reserve
Robanda
Lake
Victoria
Western Corridor
Serengeti National Park
N
0
15
30
60 Kilometers

Figure 1.



18
16
14
12
10
8
6
4
2
0
%
Cattle
Goats
Sheep
Newborn
Bought
Diseases
Grazing
Depredation
Theft
Sold
Slaughtered
Recruitment
Livestock loss/gain factors

Figure 2.

Paper IV

Spatial-temporal variation in meat and fish consumption among humans in the western Serengeti, Tanzania: the importance of migratory herbivores

Running headline: meat and fish consumption in Serengeti

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Abstract

Illegal bushmeat hunting has become a serious problem for wildlife managers in many African countries. We investigated the spatial and temporal pattern in meat and fish consumption by people surrounding the Serengeti National Park, Tanzania to further understand the links between hunting and consumption. We studied 150 households in five villages during March – December 2006, along a gradient from the National Park boundary up to 80 km away. In addition, two parallel 10 km transects were conducted monthly near three villages closest to the national park in order to investigate the relationship between household meat consumption and the influx of migratory herbivores. We found that the number of meat meals was higher in the villages closest to protected areas. The weekly number of meat meals per household in all villages within 30 km from the national park boundary increased with the influx of migratory herbivores. Moreover, meat consumption was unrelated to income, except in the most distant village were there was a positive correlation. The number of fish meals in the closest villages to the national park decreased with the influx of migratory herbivores. We recommend a coordinated management of fish harvesting from Lake Victoria and wildlife conservation around the Serengeti National Park to implement a sustainable management of the two ecologically different natural resources in the future.

Introduction

Since immemorial time, local communities have relied heavily on use of natural resources such as water supply, forest products, grazing land, firewood and bushmeat. Bushmeat, derived from wild animals, is an important source of cheap protein for African and Latin American societies where in some countries (i.e. Liberia) up to 75% of total meat consumed is derived from wild animals (e.g. Anstey, 1991; Barnett, 2000; Rao & McGowan, 2002). An extensive use of bushmeat has been well documented in West and Central Africa (Fa *et al*., 2003; Wilkie *et al*., 2005). Although the issue has received much less attention in East and Southern Africa, studies suggest that illegal bushmeat hunting has developed to become a serious problem for wildlife managers, because of a growing demand for bushmeat, burgeoning human populations (e.g. the human populations of Kenya and Tanzania increased from 6 and 8 million in 1950 to 34 and 38 million in 2005, respectively) and increasing commercialisation of the bushmeat trade (Edroma & Kenyi, 1985; Dublin *et al*., 1990; Campbell & Hofer, 1995; Barnett, 2000; UN, 2005). For instance, in Tanzania partially protected areas (IUCN category ≥ IV) appear to be particularly hard-hit by illegal bushmeat hunting (Caro *et al*., 1998), combined with high rates of habitat degradation (Pelkey *et al.*, 2000).

Little quantitative research has been conducted on the factors that drive consumer demand for bushmeat in poor tropical countries (Wilkie & Godoy, 2001). Increases in household income appear to drive a shift in preference from bushmeat to the meat of domesticated animals. Albrechtsen *et al*. (2005) found that income was positively correlated with volume of small livestock meats consumed per household, but negatively related with bushmeat eaten. This indicates that it is the poor that rely mostly on bushmeat. However, the picture is not so clear, since Barnett (2000) reported that there is also an increasing trend for a preference for bushmeat by the affluent elite in urban areas.

In addition to wildlife, fish also is a vital source of animal protein in Sub-Saharan Africa (FAO, 2004). The great lakes of East Africa, Lake Victoria, Tanganyika and Nyasa, plays a key role in this respect. However, several studies report that catches are declining due to overexploitation, pollution and environmental degradation (i.e. exotic species introductions, water hyacinth (*Eichhornia crassipes*)) (Matsuishi *et al*., 2006; Balirwa, 2007). For example, on the Kenyan side of Lake Victoria, the important fishery on Nile perch (*Lates niloticus*) has declined steadily from a peak of 115,000 tons in 1999 to 57,000 tons in 2004, mainly due to lack of enforcement of fishing regulations and lack of involvement of local stakeholders in fisheries management that has led to overexploitation (Njiru *et al*., 2007). Similar declines due to over-harvesting have also been noted for other fish species such as Nile tilapia (*Oreochromis niloticus*) and the small indigenous cyprinid (*Rastrineobola argentea*) (Matsuishi *et al*., 2006; Njiru *et al*., 2007). The diminishing fish resource mainly due to commercial fishing operations has also negative consequences for local communities along the shores of Lake Victoria who are increasingly using smaller gill nets and in some instances illegal and destructive fishing practices to meet household needs (Balirwa, 2007).

Recently in West Africa, Brashares et al. (2004) indicated that fish and bushmeat exploitation is linked, where low regional supplies of fish caused an intensification of local bushmeat hunting. However, the direction of the linkage is debated (Rowcliffe *et* *al*., 2005), where for instance Wilkie *et al*. (2005) showed that bushmeat availability might also affect the consumption of fish. These studies strongly suggest that the unsustainable fishing and deterioration of the resource base in Lake Victoria does not only have severe implication for local communities, but might also entail serious consequences for wildlife within the bordering protected areas. There is therefore an urgent need to assess the relationship between the fish and bushmeat resources in the lake region and their role in human welfare.

In this study we therefore focused upon the relationship between the consumption of fish and bushmeat among villages bordering Lake Victoria and the Serengeti National Park (SNP), Tanzania. By conducting transects within different parts of the national park, we investigated how the seasonal presence of high densities of chiefly migratory herbivores and other socio-economic factors affected consumption levels by using villages along a gradient from the resource source (i.e. lake or park).

Methods

Study area

Climate and large mammals

This study was conducted in the north-western part of the Serengeti National Park (SNP) (Fig. 1) between March and December 2006. The SNP (14,763 km^2) is the largest park in Tanzania. In the west the park is bordered by Ikorongo Game Reserve (ca. 563 km^2), Grumeti Game Reserve (ca. 416 km^2) and the Ikoma Open Area (ca. 600 km^2) that act as buffer zones between the park and the village areas. The common large resident herbivores in the area include giraffe, buffalo, topi (*Damaliscus korrigum*) and impala (*Aepyceros melampus*). The western corridor of the SNP is characterised by the annual wildebeest migration, which in June – August moves through the partially protected and village areas on their way north (Thirgood *et al*., 2004). In addition to the migratory herbivores there is also a resident population of wildebeest in the western corridor, that move towards Lake Victoria during the wet season (Maddock, 1979). However, the populations of the resident herbivores in the game reserves are relatively low probably due to high levels of illegal bushmeat hunting (Campbell & Hofer, 1995; Rusch *et al*., 2005).

Local people and livelihoods

Human population density is high (70 people / km^2) in the north-western Serengeti, with an annual growth rate of 2.5% between 1988 and 2002 (URT, 2002). The economy of local communities is mainly based on subsistence farming and livestock husbandry. However, erratic rainfall, poor soils, tse tse fly infestation makes farming and keeping livestock very difficult, and alternative sources of protein are therefore vital. For the villages adjacent to Lake Victoria fishing is considered important, where fish species like Nile perch, tilapia and the small indigenous cyprinid (locally called dagaa) dominate the catch. Fishing is done mainly with small gill nets from dug out canoes throughout the year. Fishing in Lake Victoria is not legally restricted and there is no limitation on the number of boats or gears used (Cowx *et al.*, 2003). In addition to fish, many of the subsistence farmers and livestock keepers surrounding the SNP also rely on bushmeat hunting in terms of food security and income generation (Loibooki *et al.*, 2002; Holmern *et al*., 2002; Kaltenborn *et al*., 2005).

In the areas outside the park trophy hunting as well as resident legal hunting is carried out. Legal offtake is low because quotas are set conservatively (Holmern *et* *al.,* 2004). On the other hand, illegal bushmeat hunting originating from the local communities in the west is very common. The great majority of arrested hunters in the protected areas come from villages within 45 km from the closest boundary (Campbell & Hofer, 1995; Holmern *et al*., 2007). The main hunting method is the use of wire snares, but also other methods are being used (Arcese *et al.,* 1995; Holmern *et al.,* 2006). Bushmeat is commonly sun dried before being transported on foot to the villages. The hunters use dried meat for home consumption, to sale in order to generate income and/or to barter for other commodities (Loibooki *et al*., 2002; Kaltenborn *et al*., 2005). An estimated 53,000 people are involved in illegal hunting, including both hunters and porters that transport the meat out of the protected areas (Loibooki *et al*., 2002). The annual offtake of meat from the ecosystem has been estimated at approximately 11,950 tons (Hofer *et al*., 1996).

Data collection

Five villages were randomly selected along a gradient of distance from the SNP boundaries. Three villages, Robanda, Nyamakendo and Nyatwali, were located within 10 kilometres from the park, with Nyatwali also being located near to Lake Victoria (see Fig 1). Thirty households were randomly selected from the list of households from each village office. Household was defined as including all people in the living quarters that permanently lived there (where we used last name to identify temporary visitors in the household). Every household was visited once a month and was requested to produce the data on the number of meals that consisted of meat, fish and vegetables during the last week preceding the visit.

During the pre-testing of the questionnaire it was noted that most households were unable to remember the amount of meat (in kg) they had bought or consumed and in some cases some butchers did not have the weighing machines (i.e. relied on hand estimates). Moreover, in most local markets, fish were sold as individuals or as bulk and sometimes sold per volume using specified containers. We therefore solely collected information on the number of meals of fish and meat. Several questions were asked before raising the meat consumption issue. This was important due to the sensitivity of this subject to local communities. It was initially attempted to differentiate between legal meat and illegal bushmeat, but it was not possible due to deep reluctance among the respondents to talk about bushmeat hunting. However, a significant proportion of meat consumed in rural Africa is usually bushmeat (Barnett *et al*., 2000). Each household member was allowed to enter the discussion as it was previously noted that one member may not remember well the number and type of meals they had been eating in the previous seven days and/or might not be at home every day. Children were encouraged to join the discussion because in most cases they are at home and literally consume every meal prepared. Relying partly on responses from children in order to get an unbiased result has also been used by others (Haule *et al*., 2002). The questionnaire also included general information on the household size (number of people), age (of respondent), sex, occupation status, education level, number of livestock (physically counted in the boma) and the monthly household income (the average estimated from three consecutive month's income).

In order to investigate the relationship between the number of meat meals the households consumed and influx of migratory herbivores, two parallel transect lines (each spaced one kilometre apart) were established at Robanda, Nyamakendo and Nyatwali sampling sites. These were run once each month. Each transect line was 10 km long. All animals sighted within 200 metres on either side of a vehicle were recorded for subsequent density calculation. We counted only herbivores because these are the targeted species of illegal bushmeat hunting, but we excluded elephants (*Loxodonta africana*) because they are not usually killed for bushmeat. Moreover the animals were placed into two groups according to their seasonal movement within the ecosystem. The migratory group included wildebeest, zebra, eland (*Taurotragus oryx*), and Thomson gazelle (*Gazella thomsoni*); the remaining herbivores were grouped as resident animals. All the three transect originated from the boundary and was driven towards the interior of the park. The animals were counted three hours after and before dawn and dusk, respectively.

Statistical analyses

Differences between samples were tested using non-parametric tests due to non-normality in distribution. We also used Pearson correlation to explore the correlation between explanatory variables. We used linear-mixed models, to account for the spatial pseudo-replication of households within the villages, in order to explore the variables influencing the number of meat and fish meals in the households during the study period (10 months), with village set as a random effect (see Crawley, 2002). The predictor variables included in the models were: livestock numbers, distance to resource (in km), household size (HH size), monthly income (income) and education (none, primary, secondary/college). The same was done for the analysis on fish meals where the variable distance to resource was calculated from the Lake shore. Since the use of stepwise multiple regression in ecology has been criticised for having several drawbacks (Whittingham *et al.*, 2006), we instead used an information theoretic approach which allows for several competing models to describe the data. We evaluated the strength of evidence for the model based on Akaike Information Criterion corrected for small samples (AIC_c) following Burnham and Anderson (2002), and selected the most parsimonious model with highest Akaike weights (ω_i). The Akaike weight indicates the probability that the model is the best among the whole set of candidate models and was used to compare the relative performance of models rather than only absolute AIC_c. The analyses were performed using SPSS 14.0 (SPSS, 2001) and R 2.3.0 Software (R Development Core Team, 2006) with significant levels set at 0.05. We reported ± 1 standard deviation (SD) throughout, except for the linear mixed effect models where SE is used.

Results

Household characteristics and consumption

Generally, the studied local communities had many similar socio-economic characteristics (Table 1 and Table 2). Across the five villages the number of meat meals were higher in the villages located close to the SNP boundary (Kruskal-Wallis, $H = 85.2$, $df = 4$, $p = 0.0001$). Similarly, there was a significant difference in the number of fish meals between villages (Kruskal-Wallis, $H = 79.9$, $df = 4$, $p = 0.0001$) where the villages close to Lake Victoria had the highest number of fish meals. The household size had a negative effect on fish consumption in Nyatwali village although the same variables positively influenced the consumption of fish in Rwamkoma village ($r_p = -0.372$, $n = 30$, $p = 0.043$; $n = 30$, $r_p = 0.370$, $p = 0.040$, respectively). Furthermore, in Kowak village there was a significant positive correlation between income and meat consumption (r_p = 0.521, n = 30, p = 0.003). Whereas none of the tested variables had any influence on meat consumption in Robanda village (Table 1).

The influence of migratory and resident herbivores

Households who were close to the SNP but far from Lake Victoria consumed more meat and less fish during the influx of migratory herbivores. Mean weekly household meat consumption at Robanda, Nyatwali, Nyamakendo and Rwamkoma villages increased when the densities of migratory herbivores increased (Robanda: r_p = 0.920, n = 10 months, p < 0.001; Nyatwali: r_p = 0.711, n = 10 months, p = 0.021; Nyamakendo: r_p = 0.953, n = 10 months, p = 0.0001; Rwamkoma: r_p = 0.682, n = 10 months, p = 0.03; Kowak: r_p = -0.100, n = 10 months, p = 0.783) (Fig 2 a-e).

In contrast fish consumption was negatively correlated to the densities of migratory herbivore close to Robanda, Nyamakendo and Rwamkoma villages (Robanda: r_p = -0.684, n = 10 months p = 0.029; Nyamakendo: r_p = -0.684, n = 10 months, p = 0.030; Rwamkoma: r_p = -0.813, n = 10 months, p = 0.004). No significant correlation was found between mean household fish consumption and densities of migratory herbivores for Nyatwali and Kowak villages (r_p = 0.538, n = 10 months, p = 0.109; r_p = 0.247, n = 10 months, p = 0.492, respectively). In all villages, the mean household fish consumption were uncorrelated to the densities of resident herbivores (Robanda: r_p = -0.289, n = 10 month, p = 0.418s; Nyatwali: r_p = -0.293, n = 10 months, p = 0.412; Nyamakendo: r_p = 0.260, n = 10 months, p = 0.464; Rwamkoma: r_p = -0.613, n = 10 months, p = 0.059; Kowak: r_p = 0.329, n = 10 months, p = 0.354).

Factors affecting the consumption of meat and fish

There were two models that had a Δ AIC_c<2 in the analysis on meat consumption (Table 3). The most parsimonious model included the variables livestock and distance to the protected area, where increasing livestock numbers led to a higher consumption, whereas increasing distance to the protected area decreased the number of meat meals (Table 3 and 4). The predictor variables present in the most parsimonious model also ranked high in importance (Table 5) when we summed AIC_c weights of models containing them over the whole set of candidate models. In the analysis on fish consumption, there were also two models that had a Δ AIC_c<2. The most parsimonious model here included both the variable distance to Lake Victoria and distance to the protected area. Here both increasing distance to Lake Victoria and the protected area reduced the number of fish meals in households, these variables also ranked high in importance (Table 5).

Discussion

Our results suggest that households that are close to protected areas consume more meat during the period of the migration than those located farther away where the peak meat consumption in the villages that were close to SNP corresponded to the peak influx of migratory herbivores. Moreover, increased supply of fish did not seem to reduce consumption of meat when this was readily available. In most villages income did not influence meat consumption, only in the most distant ones.

Although our data cannot distinguish between the legal and illegal sources of consumed meat, the positive correlation between influx of migratory herbivores and the mean number of meat meals consumed in the villages that were close to the park boundary suggest an extended utilization of bushmeat during this period. This interpretation is further supported by other studies, which show that rural residents (and increasingly even in urban areas) rely to a large extent on bushmeat for most of their animal protein (Barnett, 2000; Fa *et al*., 2003; Albrechtsen *et al*., 2005). However, one of the study villages (i.e. Robanda) is included in the Serengeti Region Conservation Program (SRCP) game cropping scheme, but this operation has very low quotas that are unlikely to impact the results (Holmern *et al*., 2002; 2004). Since extremely few residents have had a license to hunt, it may be assumed that the excess meat consumed in the villages that were close to SNP during the influx of migration was illegally obtained. This is supported by the observation of meat consumption at Kowak village that was about 80 km from the park boundary where the meat consumption increased with income and not with influx of migratory herbivores.

The seasonal availability of herbivores also affects bushmeat prices that are almost halved when the migration arrives in the village areas (Holmern *et al*., 2002). Bushmeat prices are unrelated to wildlife species, but are primarily determined by the weight of the dry meat pieces which is the most common unit of trade (Holmern, 2000; Holmern *et al*., 2002). Although there is evidence for a preference for certain bushmeat species among the different tribes (Ndibalema & Songorwa, 2007), generally the identification of species by meat taste is poor (Nyahongo *et al*., in prep.). The limited cash availability among the very poor people in this area, together with the fact that fish and domestic meat is more expensive (in the villages distant from Lake Victoria) than bushmeat, means that these alternatives cannot currently out-compete wildlife as the primary protein source.

Furthermore, the access to meat or fish sources may depend on several other factors, such as logistical difficulties because of having to circumvent impassable areas, likelihood of being arrested, the distance to travel and time to reach the profitable source area may also reduce the utility to such resources (Nyahongo *et al*., 2006). For example, the distance between Kowak village and the closest point to Lake Victoria is only 17.8 km by air (Table 2) but the access is denied due to a large area in between covered by swamp, steep hills, gullies and thick acacia bushes. Thus, people are forced to take a longer route (i.e. use the old Sirari-Musoma road, where the distance becomes approximately 60 km) to reach the closest fishing station located at Kinesi along the shore of Lake Victoria.

Mean household meat and fish consumption per month fluctuated with movement of migratory herbivores in or close to villages that were less than 30 km from the park. In the western Serengeti, it is generally known that during the influx of wildebeest migrations huge herds of animals roam through villages and agricultural lands and large numbers of animals may be slaughtered literally at the doorstep. Therefore, it is not surprising to see the higher household meat consumption during the influx of migratory herbivores. Similar higher household meat consumption was observed during the influx of migratory herbivores in the study area close to Robanda, Nyatwali, Nyamakendo and Rwamkoma villages where in some villages the peak meat consumption corresponded to the peak migration (Fig. 2a-d). There are also strong traditional cultural motives for hunting in this region (Kaltenborn *et al*., 2005), which may further influence the consumption and resistance to the introduction of alternative animal protein sources. However, the consumption of fish was relatively low in the above villages during the peak migration suggesting that bushmeat and fish may complement each other, especially in the villages that are farther from the lake but located close to the park boundary.

Concluding remarks

In order to reduce the dependence on bushmeat, alternative sources of meat protein together with some income generating projects need to be considered in the general local and national development planning. The contribution of fish to household diet as an alternative to bushmeat should be emphasized so that the limitation on processing fresh fish and transportation to local market is solved. Industrial harvesting of fish from the Lake Victoria need to be coordinated as it may reduce availability of fish to the local market in both villages located close to the lake and the distant villages and thus increasing the pressure and reliance on bushmeat. Therefore the policy markers need to understand the link and the need for coordinated management between these two ecologically very different resources.

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Biographical sketches

Julius Nyahongo is a senior research scientist with the Tanzanian Wildlife Research Institute. He is a wildlife ecologist specializing in human-wildlife interactions. He has worked intensively with human-wildlife interactions in Tanzania.

Tomas Holmern is a researcher with the Department of Biology at the Norwegian University of Science and Technology. He is interested in human-wildlife interactions and has recently been working on bushmeat hunting and local law enforcement in the Serengeti.

Bjørn Kaltenborn is a senior research scientist with the Norwegian Institute for Nature Research. He is a geographer and social scientist specializing in human-environment interactions. He has worked extensively with human-wildlife conflicts in the Nordic countries as well as in East Africa and South Asia.

Eivin Røskaft is a behavioural ecologist interested in a wide range of birds and mammals species in Europe, North America and Africa, and in human-wildlife conflicts over the use of limited land.

Table 1: Household social characteristics and mean weekly meat and fish consumption in relation to household size, wealth and level of education, distance from the park boundaries and the lake (Pearson correlation, n = 10 months)

Villages	Household social characteristics					Pearson correlation: (Pvalue, n = 10 months)							
	Level of education achieved (%)			Occupation (%)		Household size		Household wealth					
								Income		Cattle		Goats/sheep	
	No education	Primary	Sec/college	Peasant	Employed	Meat	Fish	Meat	Fish	Meat	Fish	Meat	Fish
Robanda	26.7	66.7	6.7	86.7	13.3	ns	Ns	ns	Ns	ns (18)	ns (18)	ns (18)	ns (18)
Nyamakendo	46.7	40.0	13.3	86.7	13.3	ns	Ns	ns	Ns	0.030 (27)	ns (27)	ns (23)	ns (23)
Nyatwali	33.3	66.7	0	100.0	0	ns	0.043	ns (29)	ns (29)	ns (20)	ns (20)	ns (25)	ns (25)
Rwamkoma	6.7	90.0	3.3	96.7	3.3	ns	0.040	ns	Ns	ns (29)	ns (29)	ns (25)	ns (25)
Kowak	6.7	83.3	10.0	83.3	16.3	ns	Ns	0.003	Ns	ns (28)	ns (28)	ns (24)	ns (24)
Pearson Chi-square test	0.001	< 0.0001	ns	Ns	ns								

Note: ns is non-significant; numbers in brackets indicate sample size

Table 2: Mean household size and annual income and the village distance from the park and Lake Victoria (Mean (SD))

Category	Robanda	Nyatwali	Nyamakendo	Rwamkoma	Kowak	Statistics
Mean household size (number of individuals)	11.8 (6.8)	10.6 (5.1)	9.9 (4.9)	11.4 (5.7)	11.7 (8.0)	P = 0.864
Mean household annual income (US$)	339.6 (159.6)	200.4 (356.4)	187.2 (325.2)	154.8 (283.2)	216.0 (344.4)	P = 0.157
Distance in km from the park boundaries	4	2	9	28	78	-
Distance in km from the Lake Victoria	95	0	78	37	17.8	-

Table 3 – The set of 12 candidate models for explaining the number of meat and fish meals (10 months) in the villages adjacent to the Serengeti. The models are ranked by the Akaike Information Criterion corrected for small samples (AIC_c). (K = number of parameters; Δ AIC_c = difference in AIC_c between the best model and the actual model; ω_i = Akaike weights). The most parsimonious model is on the top of the list. Analyses are based on a total of 147 households in 5 villages.

Model	**K**	**AIC_c**	**Δ AIC_c**	**ω_i**
a) Meat consumption:				
Livestock + distance to protected area	5	957.2	0.000	0.449
Livestock + distance to protected area + hh size	6	959.5	1.799	0.182
Livestock + distance to protected area + income	6	959.8	2.172	0.152
Livestock + distance to protected area + education	7	961.0	3.337	0.085
Livestock + distance to protected area + hh size + income	7	961.7	4.004	0.061
Livestock + distance to protected area + hh size + education	8	962.9	5.232	0.032
Livestock	4	965.1	7.450	0.010
Livestock + distance to protected area + hh size + income + education	9	965.1	7.462	0.010
Distance to protected area	4	965.8	8.111	0.007
Livestock + hh size	5	967.0	9.301	0.004
Livestock + income	5	967.0	9.585	0.004
Livestock + education	6	968.7	11.050	0.002
b) Fish consumption:				
Distance to Lake Victoria + distance to protected area	5	991.5	0.000	0.393
Distance to Lake Victoria + distance to protected area + hh size	6	993.4	1.916	0.150
Distance to Lake Victoria + distance to protected area + livestock	6	993.5	2.045	0.141
Distance to Lake Victoria + distance to protected area + income	6	993.6	2.136	0.135
Distance to Lake Victoria + distance to protected area + education	7	995.0	3.534	0.067
Distance to Lake Victoria + distance to protected area + livestock + hh size	7	995.3	3.857	0.057
Distance to Lake Victoria + distance to protected area + hh size + livestock	7	995.7	4.238	0.047
Distance to Lake Victoria + distance to protected area + hh size + livestock + income + education	10	1001.0	9.669	0.004
Distance to Lake Victoria	4	1001.0	10.000	0.002
Distance to Lake Victoria + hh size	4	1003.0	11.870	0.001
Distance to Lake Victoria + livestock	5	1003.0	12.010	0.001
Distance to Lake Victoria + income	5	1004.0	12.120	0.001

Table 4 – Estimate for the most parsimonious model of the number of meat and fish meals. For more details see Table 3.

Coefficients	Estimate	SE	*T*	*P*-value
a) Meat consumption:				
Intercept	27.919	2.029	13.759	<0.001
Livestock	0.052	0.016	3.206	0.002
Distance to protected	-0.218	0.052	-4.168	0.025
b) Fish consumption:				
Intercept	87.03	3.34	26.06	<0.001
Distance to protected	-0.931	0.205	-4.549	0.045
Distance to Lake	-0.742	0.155	-4.787	0.041

Table 5 – Cumulative AIC_c weights for the candidate set of models with variables that influenced meat and fish meals. The sum of AIC_C weights was calculated across all models in the confidence set where the variable (n) was present.

	Meat		**Fish**	
Variable	**n**	**Sum AIC_c weights**	**n**	**Sum AIC_c weights**
Intercept	12	1.0	12	1.0
Livestock	11	0.99	5	0.25
Distance from protected area	8	0.98	8	0.99
Distance from Lake Victoria	-	-	12	1.0
HHsize	5	0.29	5	0.259
Income	4	0.23	3	0.14
Education	4	0.13	2	0.071

Figure legends:

Figure 1. Map of the protected areas in the western Serengeti showing the villages as grey pentagons (black are the 5 study villages). The 3 transect locations are shown as grey stripes. Arrows give an illustration of some the different migratory pathways for the wildebeest. Arrow size is roughly proportional to the abundance of herds along the respective pathways. On their northward migration the wildebeest herds use parts of the Western Corridor, as well as the partially protected and village areas, depending upon the rainfall pattern.

Figure 2. Mean monthly migratory and resident herbivore densities and mean meat and fish meals consumed per week in five villages from March to December 2006.

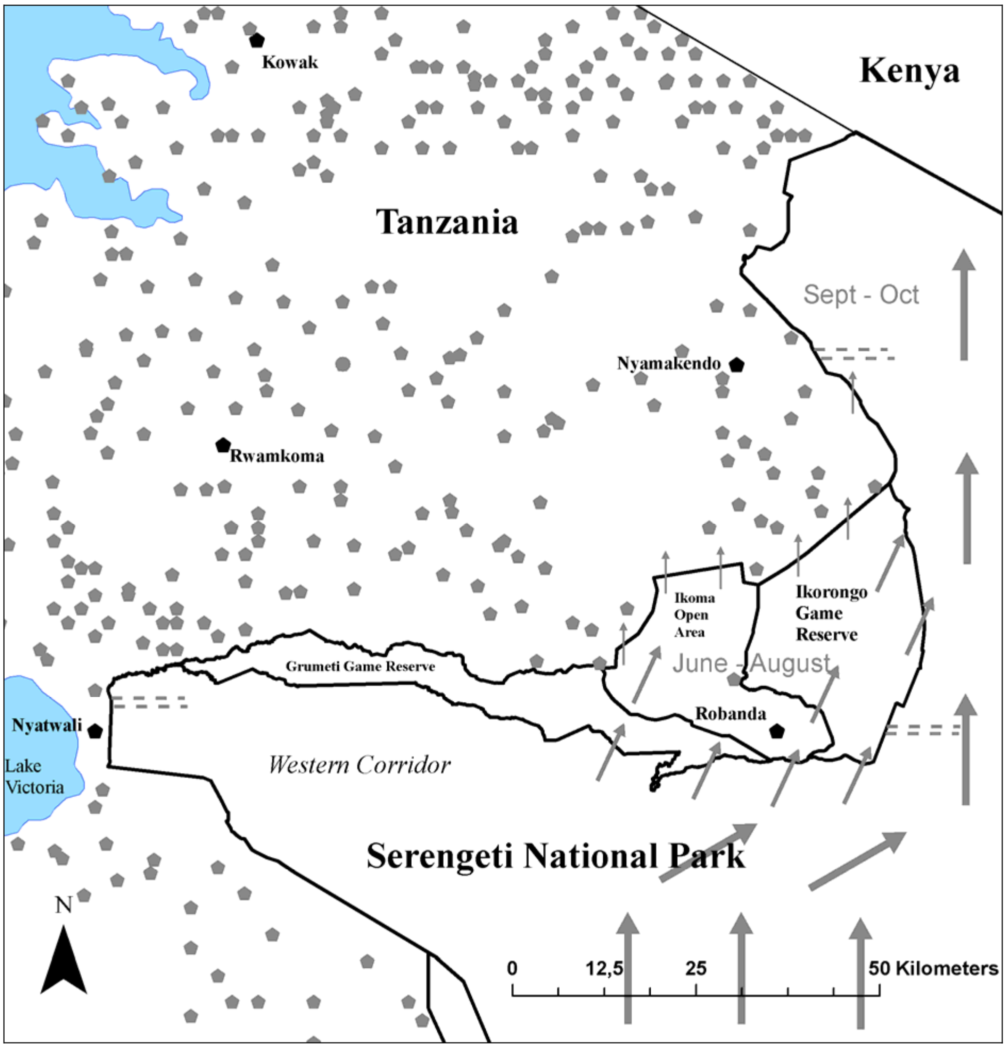
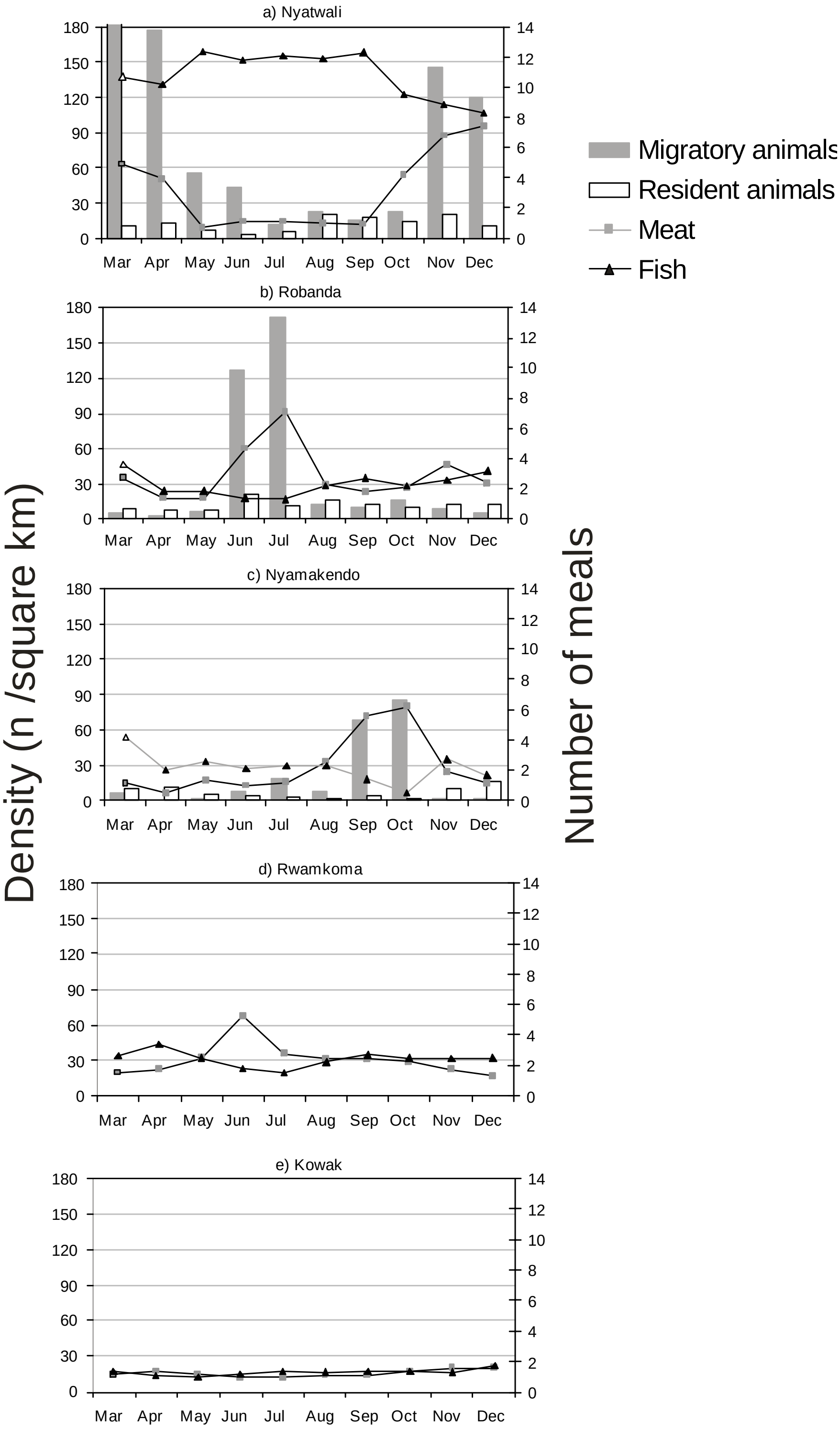

Kowak
Kenya
Tanzania
Sept - Oct
Nyamakendo
Rwamkoma
Ikoma
Open
Area
Ikorongo
Game
Reserve
Grumeti Game Reserve
June - August
Nyatwali
Robanda
Lake
Victoria
Western Corridor
Serengeti National Park
N
0
12,5
25
50 Kilometers

Fig. 1


a) Nyatwali
b) Robanda
c) Nyamakendo
d) Rwamkoma
e) Kowak
Density (n /square km)
Number of meals
Migratory animals
Resident animals
Meat
Fish
0
30
60
90
120
150
180
0
2
4
6
8
10
12
14
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

567
568 Fig. 2

Paper V

Bushmeat preference and species recognition based on meat taste by humans in the western Serengeti, Tanzania

Running headline: Bushmeat preference

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Abstract

Wildlife meat has been an important source of meat protein to human kind since pre-historical time. Even now, some African and Latin American societies survive largely on meat obtained from wild animals. We used human taste ability to rank meat preference and species recognition by providing each test-person with boiled pieces of meat from different wild ungulates (topi, impala, zebra and wildebeest) and beef. Nine-hundred test-persons of different age and sex from nine selected villages in the western Serengeti were included in the experiment. Every test-person was provided with a piece of meat from two of the above mentioned species, yielding 10 groups with 90 persons in each. In order of preference, beef was most preferred followed by topi, impala, zebra and wildebeest. In logistic regression analyses, we investigated the possible influence of age, sex and distance from national park boundaries on meat preference and species recognition. Generally, distance explained a significant amount of variation in meat preference and species recognition in most two-species comparisons. In addition, sex explained some of the variation in preference in the impala-wildebeest, zebra-wildebeest and beef-zebra comparisons. Overall, identification of species by meat taste was poor. The most identifiable meat was beef and the least was impala. A combination of reduced beef prices and improved wildlife management including discouragement of local people the bushmeat supply, could encourage more domestic meat utilization and reduced hunting pressure on resident wild herbivores in Serengeti.

Key words: Bushmeat, meat taste, preference ranks, Serengeti

Introduction

Before the onset of agriculture (about 10 000 years B.C., Diamond, 2005), the killing of wild animals for food and survival purposes was one of the most important social activities of the pre-historical *Homo sapiens* (Blain, 2005). Even presently, some African and Latin American societies survive mainly on meat obtained from wild animals (bushmeat) (e.g. Bennet, 2006; Rao and McGowan, 2002). Bushmeat derived from wild animals by local communities has, in modern times, become easy due to efficient hunting techniques such as the use of guns and wire snares (Blain, 2005). In Africa, the extensive utilization of bushmeat is well documented in some western and central African countries (Barnett, 2000; Fa et al*.,* 2003; Wilkie et al., 2005). However, bushmeat is often obtained illegally inside protected areas (Hofer et al., 1996; Loibooki et al., 2002; Holmern et al., 2002). Such illegal bushmeat utilization has resulted in a serious conflict between conservation priorities and priorities of local communities surrounding such protected areas (Campbell and Hofer, 1995). One important question is whether current offtake will ensure future sustainability of bushmeat species as demand increases due to a rapidly growing human population. This situation is not only causing widespread depletion of wildlife populations but also enhances encroachment on their habitats (Bodmer, 1994; Alvard et al*.,* 1997; Barnett 2000; Loibooki et al*.*, 2002; Rao and McGowan, 2002; Fa et al*.,* 2003).

Generally, many species are utilized for bushmeat and species selection within particular areas depends largely on location, habitat type and availability (Barnett, 2000). In most African countries, targeted species include insects, reptiles, birds and mammals of various species including primates (FitzGibbon et al*.,* 1996; Noss, 1998;

Stein, 2001; John et al., 2003). In Serengeti, northern Tanzania, the common large herbivore species usually utilized for bushmeat include wildebeest (*Connochaetes taurinus*), Cape buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), zebra (*Equus burchelli*), eland (*Tragelaphus orxy*), Thomson gazelle (*Gazella thomsonii*), Grant gazelle (*G. granti*) and giraffe (*Giraffa camelopardalis*). Other species include topi (*Damaliscus korrigum*), kongoni (*Alcelaphus buselaphus*), warthog (*Phacochoerus aethiopicus*), waterbuck (*Kobus ellipsiprymnus*), bush buck (*Tragelaphus scriptus*) and ostrich (*Struthio camelus*) (Campbell and Hofer, 1995; Hofer et al., 1996; Mduma et al., 1998; Holmern et al., 2004).

Generally, studies on bushmeat utilization have mostly been concerned with the identification of utilized species (Barnett, 2000), dietary contribution of bushmeat to the local people, the cost incurred and profit obtained from the sale of bushmeat. Moreover, some studies have related bushmeat utilization directly to the loss of biodiversity while others have related the human population growth and thereby habitat destruction to the loss of bushmeat species. Yet, some studies have suggested that the contribution of bushmeat may be an important factor in poverty reduction in the rural areas (see, Campbell and Hofer, 1995; Hofer et al., 1996; McKinney, 2001; Haule et al., 2002; Loibooki et al., 2002; Rao and McGowan, 2002; Fa et al., 2003; Rowcliffe et al., 2003; Wilkie et al., 2005; Bennett et al., 2006; Nyahongo et al., 2006).

Currently, two-thirds of African people (615 million) live in small-scale, low productivity farms and are facing food insecurity that affect 194 million people, most of them being children (Conway and Toenniessen, 2003). Factors that contribute to the food insecurity in Africa include poor distribution of farm products, soil fertility, crop losses due to diseases, pests, and international trade policies such as quota systems, tariffs and subsidies as well as abiotic stress (Orr and Mwale, 2001; Pretty et al., 2002; Rao and McGowan, 2002; Conway and Toenniessen, 2003). In addition, the affordable technological innovations such as improved seeds and fertilizers and capital (human capital, natural capital, produced capital, social capital and cultural capital) are lacking due to abject poverty in Africa (Bebbington, 1999; Conway and Toenniessen, 2003). For the local communities surrounding the western Serengeti, like many other poor African communities, relying on bushmeat hunting is considered important for food security and income generation (Loibooki et al., 2002; Holmern et al., 2004; Kaltenborn et al., 2005).

Nevertheless, a study on species preference as a result of meat quality and species identification based on meat taste has not been carried out though this might be important in order to conserve the most preferred ungulate species in a sustainable way. Moreover, establishment of game ranches in order to provide alternative meat sources to domestic meat may require knowledge on preference, palatability and acceptance based on perceived taste quality (flavour). In addition, studies that may link illegal bushmeat hunting and local market demand for certain species of ungulates based on perceived meat taste quality may also require prior knowledge on meat quality, species preference and acceptability.

The aim of this study was to answer two basic questions: 1) Do local people have specific species preference patterns based on meat taste? 2. Are local people capable of identifying species of animals by meat taste? Related to the two main questions, the following three hypotheses were tested: i) People from villages close to the park boundary have long experience with bushmeat species and have eaten more meat from different bushmeat species, hence they are more capable of recognizing different species by meat taste than people from distant villages. ii). Women have more experience preparing meat for food and also do most family cooking, hence they have a certain preference pattern for different species and they are able to identify the bushmeat species by meat taste more correctly than men. iii) Adult people have more experience with bushmeat species and are therefore able to rank the meats and can recognize the species by meat taste more correctly than younger people.

Methods

Study area

The current study was carried out in villages surrounding the north-western part of the Serengeti National Park (here after referred to as “national park”) (Fig. 1) in northern Tanzania, between July and December 2006. The SNP (14,763 km^2) established in 1951, is a World Heritage Site (1981) and the largest national park in Tanzania. Ikorongo Game Reserve (ca. 563 km^2), Grumeti Game Reserve (ca. 416 km^2) and the Ikoma Open Area (ca. 600 km^2) act as buffer zones between the park and the village areas to the north-west. The average annual temperature in the study area is 21.7^{o}C, with an average annual precipitation of 800 mm in the eastern part to 1050 mm in the western parts. The most common large resident herbivores in the area are: giraffe, buffalo, topi, impala and the gazelles, *Gazella sp*. The western Serengeti experiences the annual wildebeest and zebra migration in June–July that moves through the partially protected and village areas on their way north (Sinclair, 1995; Thirgood et al., 2004). However, the populations of the resident herbivores are relatively low in the buffer zones and in the open areas probably due to illegal bushmeat hunting (Rusch et al., 2005).

Local people and livelihoods

In western Serengeti the human population density is relatively high (70 people/km^2) experiencing an annual growth rate of 2.5% between 1988 and 2002 (URT, 2002). Village areas are made up of small units consisting of widely dispersed houses with no clear cut border between the household areas within and between villages. The economy of local communities is mainly based on subsistence crop farming and livestock husbandry that consist of cattle, goats and sheep though a few farmers also keep donkeys and pigs (Loibooki et al., 2002). The human population density within a 45 km belt from the park is relatively high partly due to immigration from other distant villages with the intention of free access to natural resources (Campbell and Hofer, 1995).

Illegal bushmeat hunters from adjacent local communities essentially use wire snares to capture wild herbivores for bushmeat (Loibooki et al., 2002). Such meat is commonly sun dried before transported to the villages on foot from protected areas (Hofer et al., 2000). The hunters use dried meat for home consumption, sale to generate income, or bartering with other commodities (Hofer et al., 2000; Loibooki et al., 2002; Kaltenborn et al., 2005). The majority of captured herbivores are large migratory species such as wildebeest and zebra. An estimated 53,000 people are involved in illegal hunting, including both hunters and porters that transport the meat out of the protected areas (Loibooki et al., 2002).

Data collection

Nine villages were selected based on the distance from the national park boundary. Robanda, Nyamakendo and Nattambisso (here after referred to as “immediate”) villages were located within 10 kilometres from the park boundaries. Rwamkoma, Busegwe and Butiama (“intermediate”) villages were located about 40 km from the park, while Kowak, Chereche and Omuga (“distant”) villages were situated more than 80 km from the park. All distances are given as shortest air distance from villages to the national park boundaries.

A visit to each village office prior to the meat taste experiment was done in order to discuss the essence of the experiment with local leaders and elaborate how the meat should be obtained and prepared. Moreover, we asked village leaders to help in convincing people to attend to the meat taste experiment.

Meat from similar parts of the two different species was compared by giving test-persons two pieces of boiled meat; one from each species. Meat used in the experiments were obtained from two sources; beef was bought from local markets while meat from wild animals were obtained by shooting eight mature males (two animals from each species) from the following species: wildebeest, topi, impala and zebra between July and December 2006 in Ikoma and Sibora Game Control Areas. The hunting was carried out by professional hunters from Grumeti Reserve Fund and game rangers from Grumeti - Ikorongo Game Reserves. The hunting operations were done carefully; no untargeted animal was killed or injured. The shot animals died instantly and were immediately skinned, and carcasses were thereafter stored in a cold room (-15^{o}C) for subsequent meat taste experiments.

Meat chopped from hindquarters of the carcasses were cut into small pieces and boiled under constant temperature and pressure for 30 minutes. To control for the effect of meat size on boiling time, we counted pieces of meat that were roughly equally cut and in each pot we placed 120 small-cut pieces. Equal volume of water (i.e. 500 ml) was added to boil the meat and equal weight of salt (one tea spoonful) was added to season it. The temperature was maintained by adjusting the gas cooker knob that controls the flame intensity while the pressure was maintained by placing a lid tightly on the cooking pot. Experiments started after two sets of meat from two different species were boiled. We recorded age and sex of the test-persons and village location in relation to the distance from the national park preceding the meat test. Before introducing the first piece of meat to test-persons, we provided them with clean water to rinse their mouths in order to remove any food remnants from previous meals. We repeated the same procedure after swallowing the first piece of meat.

The test-persons, who voluntarily came to test meat, were asked to line-up in three different lines based on age and gender. This arrangement was important to encourage more women and children who were shy to mix with adult men. Only the researcher had knowledge of which species that was tested at any time. After each test-person declared that he or she had swallowed the second piece of meat (which was done randomly), we asked him or her to tell us, based on the meat taste, which of the two pieces tasted best. We recorded each individual’s opinion and thereafter we requested each test-person to identify the species whose pieces of meat were tasted (choice of two species). Similar experiment and approach was repeated for all different combinations of animals under study and in all nine randomly selected villages (30 test-persons for each two-species comparisons in each of the three village categories based on distance to the national park).

Statistical analyses

Differences between samples were tested by using non-parametric tests due to non-normality in distribution. Within each two-paired comparison, forward-step-wise binary logistic regression analyses were carried out to investigate the influence of age (children versus adults), gender and distance from the park (immediate, intermediate and distant villages) and their interactions (independent variables) on meat preference and species recognition (dependent variables). For all tests $p < 0.05$ was considered significant. All analyses were performed using SPSS 14.0 statistical package (SPSS, 2005).

Results

General characteristics of test-persons

Overall, 900 test-persons participated in the study, 300 from each of the categories “immediate”, “intermediate” and “distant” villages. The socio-economic characteristics of the test-persons are provided in Table 1.

Species preference by meat taste

Overall preference

Regardless of distance from the park, age and gender, the meat that scored the highest overall preference rank in the two-species comparisons was beef, closely followed by topi and impala. Zebra and wildebeest were least preferred taste trials per species, Table 2). Overall, distance from the park reduced the preference of topi

(Pearson Chi-square: $p < 0.001$), impala and zebra. Distance, age or gender did not affect the preference for the remaining species (Table 3).

Regardless of age and gender, topi scored the highest rank followed by beef in the immediate villages while impala and wildebeest were less preferred. The least preferred animal species in the immediate villages was zebra (Table 2). In the immediate villages only gender had significant effect on the preference for zebra (Pearson Chi-square: $p = 0.037$ (Table 3), whereas females preferred zebra than men (mean rank for men = 63.3, n = 83; mean rank for women = 54.2, n = 37; Wilcoxon Sign Rank: W = 2007.0, $p = 0.037$. Age and gender had no significant effect on preference for the other species in the immediate village (Table 3).

In the intermediate villages, impala meat was highly favoured followed by beef. Topi and zebra were less preferred. The least favoured species was wildebeest (Table 2). Age and gender had no significant effect on meat preference in intermediate villages (Table 3).

In distant villages, the most favoured meat was beef followed by impala. Topi ranked the third while wildebeest and zebra scored below average (Table 2). Age and gender had no significant effect on meat preference in distant villages (Table 3).

Predictors explaining variation in preference in specific two-species comparisons

Beef-topi

Overall, there was no statistical difference in test-persons preferring beef (46) over topi (44) (Wilcoxon Sign Rank, W = -1.42, n = 90, $p = 0.833$). In the logistic regression analysis, none of the independent variables could explain the variation in preference.

Beef-impala

Overall, test persons preferred beef (59) over impala (31) (Wilcoxon Sign Rank, W = -2.951, n = 90, p = 0.003). In the logistic regression analysis, none of the independent variables could explain the variation in preference.

Beef-wildebeest

Overall, test persons preferred beef (73) over wildebeest (17) (Wilcoxon Sign Rank, W = -5.90, n = 90, p < 0.001). In the final regression model, the only variable that was significant predictor of differences in meat preference was distance to the park boundary (Table 4), and 81.1% of the cases were classified correctly by using this model. Removing this variable resulted in a significantly poorer fit of the model (change in -2 log likelihood = 8.82, df = 2, p = 0.012). Although test persons in all three villages preferred beef over wildebeest, more inhabitants of immediate villages preferred wildebeest (36.7%, n = 30) than those further away (both 10.0%, n = 30 in both cases).

Beef-zebra

Overall, test-persons preferred beef (64) over zebra (26) (Wilcoxon Sign Rank, W = Wilcoxon Sign Rank, W = -7.48, n = 90, p < 0.001). In the final regression model, the interaction between distance and gender were significant predictors of differences in meat preference (Table 4), and 78.9% of the cases were classified correctly by using this model. Removing this variable resulted in a significantly poorer fit of the model (change in -2log likelihood = 16.51, df = 2, p < 0.001). Test-persons in the immediate and distant villages preferred beef over zebra (80.0% and 86.7%, respectively, n = 30 in both cases), while inhabitants of intermediate villages generally preferred zebra

(53.3%, n = 30). Moreover, in the intermediate villages, females preferred zebra (88.9%, n = 9) while men preferred beef (61.9%, n = 21). Both sexes in the immediate and distant villages preferred beef (immediate: females 70% (n = 10), males 85 (n = 20); distant: females 100% (n = 5), males 84% (n = 25)), but in general (all distances), females preferred zebra more (45.8%, n = 24) than males (22.7%, n = 66).

Topi-impala

Regardless of the distance from the park, age or gender, test-persons preferred topi (57) over impala (33) (Wilcoxon Sign Rank, W = -2.53, n= 90, p = 0.011). In the final regression model, distance to park boundary was a significant predictor of differences in meat preference (Table 4), and 76.7% of the cases were classified correctly by using this model. Removing this variable resulted in a significantly poorer fit of the model (change in -2 log likelihood = 23.33, df = 2, p < 0.001). Topi was preferred in immediate (86.7%, n = 30) and intermediate villages (73.3%, n = 30) while impala was preferred in the distant villages (70.0%, n = 30).

Topi-wildebeest

Regardless of the distance from the park, age or gender, test-persons preferred topi (61) over wildebeest (29) (W = Wilcoxon Sign Rank, W = -5.66, n = 90, p < 0.001). In the final regression model, the only variable that was significant predictor of meat preference was distance to the park boundary (Table 4), and 81.1% of the cases were classified correctly by using this model. Removing this variable resulted in a significantly poorer fit of the model (change in -2 log likelihood = 29.91, df = 2, p < 0.001). Test-persons in the immediate and intermediate villages preferred topi (immediate: 83.3%, n = 30; intermediate: 90.0%, n= 30), while those in distant villages preferred wildebeest (70.0%, n = 30).

Topi-zebra

Overall, test-persons who participated in the meat taste experiment preferred topi (62) over zebra (28) (Wilcoxon Sign Rank, W = Wilcoxon Sign Rank, $W = -3.24$, $n= 90$, $p < 0.001$). Distance from the park boundary was the only independent variable in the final regression model that significantly predicted the meat preference (Table 4), whereas 80.0% of the cases were classified correctly by using this model. Removing this variable ("distance") resulted in a significantly poorer fit of the model (change in -2 log likelihood = 28.74, $df = 2$, $p < 0.001$). The test-persons in the immediate (93.3%, $n = 30$) and distant (80.0%, $n = 30$) villages preferred topi, while those in intermediate villages preferred zebra (66.7%, $n = 30$).

Impala-wildebeest

Overall, test-persons, regardless of the distance from the park boundary, age and gender, preferred impala (66) over wildebeest (24), (W = Wilcoxon Sign Rank, $W = -4.43$, $n = 90$, $p < 0.001$). In the final regression model, the distance from the park and the interaction between distance and gender of test-persons were significant predictor of the meat preference, whereas 78.9% of the cases were classified correctly by using this model (Table 4). Removing these variables ("distance and gender-distance interaction") resulted in a significantly poorer fit of the model (change in -2 log likelihood = 17.41, $df = 4$, $p = 0.002$). Although impala was preferred in all villages, the analysis suggest that test-persons in villages that were classified as immediate to the park boundary preferred impala less (56.7%, $n = 30$) than those in intermediate (83.3%, $n = 30$) or distant villages (80.0%, $n = 30$). Moreover, in the immediate villages, males preferred wildebeest (63.2%, $n = 19$) while females preferred impala (90.9, $n = 11$).

Impala-zebra

Regardless of the distance from the park boundary, test-person preferred impala (72) over zebra (18) (Wilcoxon Sign Rank, W =,-5.62, n=90, $p < 0.001$). Distance from the park boundary was the only independent variable in the final regression model that significantly predicted the meat preference (Table 4), whereas 80.0% of the cases were classified correctly by using this model. Removing this variable (“distance”) resulted in a significantly poorer fit of the model (change in -2 log likelihood = 7.11, df = 2, p = 0.028). The test-persons in the immediate (80%, n = 30) and intermediate (90.0%, n = 40) villages preferred impala, while those in distant villages had the least preference for impala (60.0%, n = 20).

Zebra-wildebeest

Overall, there was no statistical difference in test-persons preferring zebra (48) or wildebeest (42), (Wilcoxon Sign Rank, W = -6.32, n= 90, p = 0.527). In the final regression model, the distance from the park and gender of test-persons were significant predictors of the meat preference, whereas 75.6% of the cases were classified correctly by using this model (Table 4). Removing these variables resulted in a significantly poorer fit of the model (change in -2 log likelihood = 37.02, df = 3, $p < 0.001$). Test-persons in the intermediate villages mostly preferred zebra (90.0%, n = 30), while those in the immediate (76.7%, n = 30) and distant (53.3%, n = 30) villages preferred wildebeest. Furthermore, overall, females preferred wildebeest (60.6%, n = 33), while males preferred zebra (61.4%, n = 57).

Species recognition by meat taste

Overall recognition

Generally, a correct recognition based on meat taste was poor among test-persons of different age and gender in all villages (25.9%, n = 1800 trials). For the pooled data, the most recognizable meat was beef while the least recognized species was impala (Table 2). Overall, distance from the park had reduces the recognition of all species while recognition of topi, impala and zebra increases with age (Table 3). Gender did not have effect on recognition of any species.

In the immediate village, of all test-persons, 55.8% (n = 120) were able to recognize beef (Table 2). The recognition of the remaining species scored less than 44% (n = 120 for each species). Neither age nor gender did influence the recognition of any species by meat taste (Table 3).

In the intermediate villages, 47.5% (n = 120) of all test-persons were able to recognize beef while none of the wild ungulate scored more than 30% (n = 120 for each species, Table 2). Neither age nor gender did influence the recognition of any species by meat taste (Table 3).

In the distant village, general recognition of species was relatively low (< 17%) and the meat that was highly recognized (16.7%, n = 120) was beef. The remaining wild ungulates scored 10% or less (Table 2). Age and gender had an effect on recognition of all wild ungulates in the distant village where adult male were able to recognize species than children and female. Beef was recognized similarly by all test-person of different age and sex (Table 3).

Predictors explaining variation in species recognition in specific two-species comparisons

Beef-topi

Overall, 67.8%, (n = 90) of the test persons were able to correctly recognize what species of meat was tasted. In the binary regression analysis, distance from the park was the only variable that could explain the variation in recognition (Table 5), and 70.0% of the cases were classified correctly by using this model. Removing this variable resulted in a significantly poorer fit of the model (change in -2 log likelihood = 11.52, df = 2, p = 0.003). Test-persons from the immediate villages were better able to identify the two species (53.3%, n = 30) than test-persons from the intermediate (30.0%, n = 30) and distant (13.3%, n = 30) villages.

Beef-impala

Overall, 24.4% (n = 90) of the test-persons were able to correctly recognize what species of meat were tasted. In the binary regression analysis, distance from the park was the only variable that could explain the variation in recognition (Table 5), and 70.0% of the cases were classified correctly by using this model. Removing this variable resulted in a significantly poorer fit of the model (change in -2 log likelihood = 11.63, df = 2, p < 0.003). Test-persons in the intermediate villages were better in species recognition (63.3%, n = 30) than test-persons from the immediate (23.3%, n =30) or distant (30.0%, n = 30) villages.

Beef-wildebeest

Overall, 24.4% (n = 90) of the test-persons were able to correctly recognize what species of meat were tested. In the final regression model, the only variable that was a significant predictor of species recognition was distance to the park boundary (Table 5) and 77.8% of the cases were classified correctly by using this model.

Removing this variable resulted in a significantly poorer fit of the model (change in -2 log likelihood = 28.61, df = 2, $p < 0.001$). Test-persons in immediate villages were better in recognizing species than in the intermediate villages (53.3% versus 20.0%, n = 30 in both cases), and test-persons in distant villages did not correctly recognize a single piece of meat (0%, n = 30).

Beef-zebra

Regardless of the distance from the park, age or gender, only 32.3% (n = 90) of the test-persons were able to recognize the correct species by meat taste. In the final regression model, the only variable that was significant predictor of species recognition was distance from the park boundary (Table 5), and 72.2% of the cases were classified correctly by using this model. Removing this variable resulted in a significantly poorer fit of the model (change in -2 log likelihood = 12.54, df = 2, p = 0.002). Test-persons from the immediate villages were better able to recognize species (56.7%, n = 30) by meat taste than the test persons from intermediate (23.3%, n = 30) or distant villages (16.7%, n = 30).

Topi-impala

Regardless of the distance from the park, age and gender, 21.1% (n = 90) of test-persons were able to recognize the correct species by meat taste. None of the independent variables entered into the binary logistic regression analysis could explain the observed variation in species recognition between these two species.

Topi-wildebeest

Regardless of the distance from the park, age and gender, 16.7% (n = 90) of the test-persons were able to recognize the correct species by meat taste. None of the independent variables entered into the binary regression analysis could explain the observed variation in species recognition between these two species.

Topi-zebra

Regardless of the distance from the park, age and gender, 21.1% (n = 90) of the test-persons were able to recognize the correct species by meat taste. Distance from the national park boundary was the only independent variable in the final regression model that significantly predicted the success or failure of a test-person to recognize species by meat taste (Table 5), whereas 78.9% of the cases were classified correctly by using this model. Removing this variable resulted in a significantly poorer fit of the model (change in -2 log likelihood = 15.9, df = 2, $p < 0.001$). Despite the low recognition rate, the test-persons from the immediate villages were able to recognize species by meat taste better (43.3%, n = 30) than test-persons from intermediate (16.7%, n = 30) and distant (3.3% n = 30) villages.

Impala-wildebeest

Regardless of the distance from the park, age and gender, 20.0% (n = 90) of the test-persons were able to recognize the correct species by meat taste. In the final regression model, the distance from the park was the only independent variable that could explain the variation in ability of a test-person to recognize the species of animals whose meat was included in the experiment (Table 5), and 80.0% of the cases were classified correctly by using this model. Removing this variable resulted in a significantly poorer fit of the model (change in -2 log likelihood = 10.52, df = 2, $p = 0.005$). The analysis suggests that the ability to correctly recognize species decline with distance from the park boundary (immediate: 33.3%; intermediate: 23.3%; distant: 3.3%, n = 30 at each distance).

Impala-zebra

Regardless of the distance from the park, age and gender, 11.1% (n = 90) of the test-persons were able to recognize the correct species by meat taste. In the binary regression analysis, distance from the park was the only variable that could explain the variation in recognition (Table 5), and 85.6% of cases were classified correctly by using this model. Removing this variable resulted in a significantly poorer fit of the model (change in -2 log likelihood = 8.44, df=2, p < 0.015). The analysis suggests that the ability to correctly recognize species declined with distance to the park boundary (immediate: 26.7%, n = 30; intermediate: 5.0%, n = 40; distant: 0.0%, n = 20).

Zebra-wildebeest

Regardless of the distance from the park, age and gender, 35.6% (n = 90) of the test-persons were able to recognize the correct species by meat taste. In the binary regression analysis, distance from the park was the only variable that could explain the variation in recognition (Table 5), and 71.1% of the cases were classified correctly by using this model. Removing this variable resulted in as significantly poorer fit of the model (change in -2 log likelihood = 11.62, df= 2, p = 0.003. Inhabitants from the immediate villages were better able to recognize the two species (60.0%, n = 30) than inhabitants from intermediate (23.3%, n = 30) or distant villages (23.3%, n = 30).

Discussion

Our overall results show that test-persons favoured beef, followed by topi and impala. The preference patterns and the ranking position of beef, topi and impala alternated along the gradient of distance from the park suggesting high preference and acceptability of the three species by test-persons from different villages along the gradient of distance from the park boundary. Distance from the park boundary and gender-distance interactions had influence on meat preferences and subsequent species recognition by meat taste of different combinations of beef and four wild ungulates meat (Table 4). In contrast, the results indicated that most test-persons were not able to identify the species based on the meat test. Generally, the most correctly identified meat was beef while the least identified species was impala.

The test-persons included in this study were of different age and gender all having different experience with wild animals which in a way might have influenced the preference and ultimate identification of animal species based on taste, aroma and texture. Studies have shown that the meat preference may be influenced by fatty aroma, texture and taste. The meat with considerable fat marbling and soft texture is considered best (Matsuishi et al., 2001). Other studies have reported that people differ in their eating process that vary with individual breathing and chewing patterns, composition and amount of saliva, and volume of their oral cavities which may affect the taste perception (van Ruth and Roozen, 2000; Pionnier et al., 2004; Geary et al., 2004). In addition, a study suggests that the moment and completeness of the velopharyngeal closure might vary between individuals, which affect the amount of volatiles transferred to the nosal cavity affecting sensation sensitivity towards different volatile aroma components among people (Buettner and Schieberle, 2000). In addition, in some villages that were close to the park boundary, alleged illegal bushmeat hunters did not want to participate in this experiment because they consider this experiment as a trick by the government to identify the illegal bushmeat hunters. Hence, we missed their valuable experience.

Furthermore, the results we discuss might have been influenced by age and gender because the data set included more adults than children and more men than women.

The most preferred meat based on the meat taste experiment was beef. The test-persons might have favoured beef due to relatively high intramuscular fat contents in the beef carcass. Some studies reported that a zebu bull has up to 40% fat content in the dressed carcass compared with 2.5% in wild ungulates (FAO, 1992). Meat with relatively high fat content produces suitable aroma; and when this is associated with soft meat texture (tenderness) which is a characteristic of beef; the meat becomes more palatable and is highly acceptable by consumers (Matsuishi et al*.,* 2004). These two combinations; texture and fatty aroma might be the reasons for most test-persons to favour beef. Moreover, beef is locally available and can be obtained throughout the year hence people may be used to the meat and were at least able to distinguish its taste from the wild meats. Furthermore, the different types of wild fodders the wild ungulates consume and crops residues that the livestock feed on may account for the difference observed. For example, in the study area, the harvesting period lasts from July to September each year; the herdsmen take the livestock to feed on straws of the harvested maize, finger millet and/or sorghum which are relatively of high quality compared to dry and over grazed feeds in the protected areas (personal observation, 2006). Feeding on wide variety of fodders of relatively low qualities has been reported to affect the meat flavour (Duckett and Kuber, 2001).

In addition, constant vigilance and flights the wild herbivores evolved in response to predation by both wild carnivores and humans (Krebs and Davies, 1987; Caro 2005), may affect meat quality due to high muscle activities which reduces the intramuscular fat contents and finally affecting the meat aroma and texture.

In the immediate villages, topi was preferred to all other species. Because topi is a resident herbivore, the local communities close to the park boundary might have illegally utilized topi meat for many years. In fact, the Serengeti Regional Conservation Programme (SRCP) cropping operation did not include topi initially as part of the species cropped to provide legal game meat to the villages, but was later included because of substantial pressure from the villagers that said they preferred this species to that of wildebeest and zebra (Holmern et al., 2002). Moreover, a recent study in Serengeti suggested that the population of topi is declining compared to other resident herbivores, which raise the concern that illegal bushmeat hunters might have been targeting the species for perceived quality meat (Rusch et al., 2005). However, impala that is also a resident herbivore scored the highest preference rank in the intermediate villages probably due to the fact that it was a common illegally obtained bushmeat in the area or was confused with topi and/or beef. A general index of how test-persons might have confused topi and impala in the meat taste experiments can be gained from a comparison of preference and subsequent recognition of the two species in the pooled data, in immediate and intermediate villages (Table 2). This finding supports the recent observation on the preference and acceptability of different species animals in the similar area of Serengeti (Kaltenborn et al., 2006).

In contrast, the zebra and wildebeest meats were not highly appreciated (scored less than 34% in all trials for pooled data). Despite of their large populations in the Serengeti, the two species are migratory herbivores that are only in the village proximities for a period lasting for only three months each year. Although it is known that local communities utilize these species highly during the period when the animals are in the village proximities (Sinclair, 1995, Thirgood et al. 2004), the harvesting period may not be long enough to warrant a fair comparison with other resident herbivores and livestock. In addition, due to vast movement of wildebeest and zebra within the ecosystem of varying habitats, landscapes and the seasonal variation may also subject these migratory ungulates in large resource variations, predation pressure and constant flight that may affect the meat quality (i.e. marbling fat and texture).

Generally, age of test-persons did not influence the meat preference for all species we studied, suggesting that the five different meats from five different species were distinguishable and ranked specifically and that ranking patterns were independent of age but was due to meat texture and fatty aroma. In contrast, the distance from the park boundary reduced the topi preference from all topi meat taste combinations. This may be due to the fact that test-persons from the immediate villages were used to topi meat and had a relatively strong preference compared to test-persons from distant villages who might have never tasted topi meat. To the distant test-persons, the topi meat might have revealed a strange or unusual aroma and texture; hence they preferred beef that they are used to. However, it is not clear as to why the distance from the park favoured the preference of impala in topi-impala combination and impala-wildebeest combination, zebra in topi-zebra combination and in beef-zebra combination. The observed association might have occurred just by chance or impala was confused with topi and unique fatty aroma of zebra attracted test-persons from distant villages who had never tasted zebra meat.

Poor identification of species based on meat taste for all species suggest that most test-persons had either low or no experience with different types of wild meats. This can be justified by relatively high beef identification (40%, n = 360) because at least every test-person had interacted with beef quite regularly. However, studies show that taste sensitivity decreases with age and health status. For instance, old people and those who are either taking medication and/or consume excessive alcohol and/or smoke have reduced sensory stimuli (Fukunga et al., 2005). Most of people who participated in this experiment were adults whose health status and social characteristics were not established prior to this experiment.

Generally distance from the park and gender-distance interaction was significant variables in logistic regression model that tested the influence of distance, age and gender on meat preference and subsequent recognition of species by meat taste among the test-persons (Table 4 and table 5). The preference of a combination of beef and zebra and that of impala and wildebeest was possible to predict in the intermediate villages using female as predictor (Table 4). Women are the cooks of most families in Africa; hence they may prefer certain species based on their experience and the taste of the meat they cook. However, women in the immediate villages, preferred impala more compared to men from the same area that preferred wildebeest more. Likewise, the combination of beef and the four wild ungulates was possible to predict along the gradient of distance from the park while only combinations of topi-zebra and that of impala-wildebeest, impala-zebra and wildebeest-zebra was possible to predict along the gradient of distance from the park (Table 4). Distance from the park explains how test-persons had experience with different species of animals whereby the test-person from distant villages had less experience with wild ungulates but had long experience with beef.

Concluding remarks

The results obtained from this study in which meat tastes were conducted to rank the preference based on the meat quality and species recognition revealed that meat taste by humans may be useful to rank meat preferences of different ungulates although the test proved as an unsuitable approach for species recognition. The distance from the park may affect the preference rank of different animal species. In contrast, age of test-persons is not good parameters for the meat preference ranking and subsequent species recognition. A substantial number of taste-persons preferred beef and were able to identify the beef by meat taste approach. This suggests that if the price of beef is reduced and wildlife management somehow manages to limit bushmeat supply (preferably by cooperating actively with communities) many people may choose to eat more beef rather than wild ungulates. This will inevitably reduce the hunting pressure on resident herbivores. The preference of beef also highlights that outreach activities could greatly increase their impact by focusing their attention on improving services for livestock, such as cattle dips, water points and veterinary services.

Future studies on the effect of bushmeat processes before transportation to the market place is recommended. This is important because the bushmeat consumers may be used to sun-dried meat that may influence the fatty aroma and the texture in different levels among the different species. Finally, the findings from this study suggest the need for special conservation attention to resident herbivores population close to village proximities. Otherwise the long term harvest and uncontrolled illegal bushmeat hunting based on current meat preferences and habitat location may seriously deplete the resident herbivore species from their key habitats.

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Biographical sketches

Julius Nyahongo is a senior research scientist with the Tanzanian Wildlife Research Institute (TAWIRI). He is a wildlife ecologist specializing in human-wildlife interactions. He has worked intensively with human-wildlife interactions in Tanzania.

Tomas Holmern is a researcher with the Department of Biology at the Norwegian University of Science and Technology. He is interested in human-wildlife conflicts and has recently been working on bushmeat hunting and local law enforcement in the Serengeti.

Bård G. Stokke is a researcher at the Department of Biology, Norwegian University of Science and Technology. He is an evolutionary biologist and behavioural ecologist working on a wide range of birds and on human-wildlife conflicts over the use of limited land.

Bjørn Kaltenborn is a senior research scientist with the Norwegian Institute for Nature Research (NINA). He is a geographer and social scientist specializing in human-environment interactions. He has worked extensively with human-wildlife conflicts in the Nordic countries as well as in East Africa and South Asia.

Eivin Røskaft is a behavioural ecologist interested in a wide range of birds and mammals species in Europe, North America and Africa, and in human-wildlife conflicts over the use of limited land.

Table 1: The socio-demographic characteristics of test persons

Location from the park boundary	Age (in years) categories (%)		Gender (%)	
	5-17 years	18 and above years	Male	Female
Overall (n = 900)	20.5	79.5	65.7	34.3
Immediate (n = 300)	12.4	87.6	61.5	38.5
Intermediate (n = 300)	24.7	75.3	69.3	30.7
Distant (n = 300)	24.6	75.4	66.1	33.9

Table 2: Meat preference ranking and species identification by meat taste (Overall = all villages regardless of the distance from the park)

Category	Meat preference based on meat taste(%)					Species recognition by meat taste (%)				
	Beef	Topi	Impala	Zebra	Wildebeest	Beef	Topi	Impala	Zebra	Wildebeest
Overall: (n = 360)	69.7	63.3	56.1	33.0	29.7	40.0	20.0	12.0	29.7	27.8
Immediate villages (n = 120)	71.7	82.5	44.2	15.8	43.3	55.8	34.2	15.0	59.2	43.3
Intermediate villages (n = 120)	61.7	57.5	63.3	54.2	10.2	47.5	20.8	19.2	23.3	30.0
Distant villages (n = 120)	75.8	50.0	60.8	29.2	35.0	16.7	5.0	4.2	6.7	10.0

Table 3: The influences of distance, age and gender on meat preference ranking and species recognition (Pearson Chi-square test). Overall = all villages, age and gender. Overall = all villages regardless of the distance from the park). Number presented are p-value and significant effects are highlighted.

Category	Meat preference by meat taste					Species recognition by meat taste				
	Beef	Topi	Impala	Zebra	Wildebeest	Beef	Topi	Impala	Zebra	Wildebeest
Overall: (p value)										
Age (n = 360)	0.720	0.314	0.295	0.448	0.212	0.650	**0.027**	**0.003**	<**0.001**	0.236
Gender (n = 360)	0.221	0.690	0.826	0.420	0.132	0.341	0.870	0.117	0.421	0.552
Distance (n = 360)	0.519	**<0.001**	**0.012**	**0.028**	0.154	**<0.001**	**<0.001**	**0.012**	**<0.001**	**<0.001**
Immediate village:										
Age (n = 120)	0.442	0.746	0.423	0.436	0.404	0.426	0.767	0.058	0.053	0.924
Gender (n = 120)	0.649	0.597	0.798	**0.037**	0.766	0.327	0.929	0.322	0.659	0.503
Intermediate villages:										
Age (n = 120)	0.730	0.207	0.293	0.903	0.417	0.369	0.079	**<0.001**	0.619	**0.033**
Gender (n = 120)	0.330	0.450	0.779	0.524	0.581	0.937	0.886	0.469	0.163	0.308
Distant villages:										
Age (n = 120)	0.730	0.207	0.293	0.903	0.417	0.071	**<0.001**	**0.002**	**0.006**	**<0.001**
Gender (n = 120)	0.330	0.450	0.779	0.524	0.581	0.657	0.267	0.122	0.879	0.949

Table 4: Final logistic regression model of influence of distance from national park boundaries (immediate, intermediate and distant) , gender (male/female) and age (child/adult), on meat preference among villagers close to Serengeti National Park, Tanzania of five species arranged in between-species comparisons. Preference refers to overall preference of 90 test persons in each two-species comparison. Only scores of parameters included in the final model are presented. Parameter estimates (β), are presented with their standard errors (SE). Wald statistic = $(\beta/SE)^2$. Odds-ratio = exp(β), represents the ratio-change in the odds of the events of the interest for a one-unit change in the predictor. * = interaction between main effects

Species comparison	Parameter in the model	Estimate (β)	SE	Wald χ^2	P	Odds-ratio
Beef-zebra	Gender*distance			9.637	0.008	
	Gender*distance (1)	-0.470	0.749	0.394	0.530	0.625
	Gender*distance (2)	-3.397	1.100	9.539	0.002	0.033
	Constant	1.317	0.291	20.530	<0.001	3.733
Beef-wildebeest	Distance			8.289	0.016	
	Distance (1)	-1.651	0.717	5.302	0.021	0.192
	Distance (2)	-8.71×10^{-17}	0.861	1.025×10^{-32}	1.000	1.000
	Constant	2.197	0.609	13.035	<0.001	9.000
Topi-impala	Distance			19.461	<0.001	
	Distance (1)	2.719	0.669	16.533	<0.001	15.167
	Distance (2)	1.859	0.574	10.497	0.001	6.417
	Constant	-0.847	0.398	4.523	0.033	0.429
Topi-wildebeest	Distance			24.303	<0.001	
	Distance (1)	2.457	0.631	15.137	<0.001	11.667
	Distance (2)	3.045	0.727	17.519	<0.001	21.000
	Constant	-0.847	0.398	4.523	0.033	0.429
Topi-zebra	Distance			21.796	<0.001	
	Distance (1)	1.253	0.863	2.109	0.146	3.500
	Distance (2)	-2.079	0.599	12.067	0.001	0.125
	Constant	1.386	0.456	9.225	0.002	4.000
Impala-wildebeest	Distance			13.059	0.001	
	Distance (1)	-1.925	0.659	8.531	0.003	0.146
	Distance (2)	0.811	0.874	0.861	0.353	2.250
	Gender*distance			7.855	0.020	
	Gender*distance (1)	2.842	1.152	6.089	0.014	17.143
	Gender*distance (2)	-1.350	1.016	1.766	0.184	0.259
	Constant	1.386	0.456	9.225	0.002	4.000
Impala-zebra	Distance			6.743	0.034	
	Distance (1)	-0.981	0.645	2.309	0.129	0.375
	Distance (2)	-1.792	0.697	6.604	0.010	0.167
	Constant	-0.405	0.456	0.789	0.374	0.667

Wildebeest-zebra	Distance			21.244	<0.001	
	Distance (1)	-1.375	0.611	5.059	0.025	0.253
	Distance (2)	2.347	0.740	10.064	0.002	10.455
	Gender	-1.392	0.587	5.622	0.018	0.249
	Constant	0.496	0.464	1.141	0.285	1.641

Table 5: Final logistic regression model of influence of distance from national park boundaries (immediate, intermediate and distant), gender (male/female) and age (children/adult), on species recognition by meat taste among villagers close to Serengeti National Park, Tanzania of five species arranged in between-species comparisons. Species recognition refers to overall recognition of 90 test persons in each two-species comparison. Only scores of parameters included in the final model are presented. Parameter estimates (β), are presented with their standard errors (SE). Wald statistic = $(\beta/SE)^2$. Odds-ratio = exp(β), represents the ratio-change in the odds of the events of the interest for a one-unit change in the predictor.

Species comparison	Parameter in the model	Estimate (β)	SE	Wald χ^2	P	Odds-ratio
Beef-topi	Distance			9.996	0.007	
	Distance (1)	2.005	0.650	9.520	0.002	7.429
	Distance (2)	1.025	0.669	2.347	0.126	2.786
	Constant	-1.872	0.537	12.146	<0.001	0.154
Beef-impala	Distance			10.837	0.004	
	Distance (1)	-0.342	0.587	0.340	0.560	0.710
	Distance (2)	1.394	0.550	6.427	0.011	4.030
	Constant	-0.847	0.398	4.523	0.033	0.429
Beef-wildebeest	Distance			14.799	0.001	
	Distance (1)	3.636	1.082	11.295	0.001	37.923
	Distance (2)	2.178	1.105	3.885	0.049	8.826
	Constant	-3.367	1.017	10.961	0.001	0.034
Beef-zebra	Distance			11.609	0.003	
	Distance (1)	1.878	0.613	9.383	0.002	6.538
	Distance (2)	0.420	0.653	0.413	0.520	1.522
	Constant	-1.609	0.490	10.793	0.001	0.200
Topi-zebra	Distance			10.884	0.004	
	Distance (1)	3.099	1.082	8.207	0.004	22.176
	Distance (2)	1.758	1.129	2.425	0.119	5.800
	Constant	-3.367	1.017	10.961	0,001	0.034
Impala-wildebeest	Distance			6.116	0.047	
	Distance (1)	2.674	1.088	6.037	0.014	14.500
	Distance (2)	2.178	1.105	3.885	0.049	8.826
	Constant	-3.367	1.017	10.961	0.001	0.034
Impala-zebra	Distance			6.117	0.047	
	Distance (1)	19.859	8189.042	5.881×10^{-6}	0.998	4.200×10^{8}
	Distance (2)	17.745	8189.042	4.695×10^{-6}	0.998	5.087×10^{7}
	Gender	-19.378	7081.818	7.487×10^{-6}	0.998	0.000
	Constant	-20.419	8189.042	6.217×10^{-6}	0.998	0.000
Wildebeest-zebra	Distance			10.964	0.004	
	Distance (1)	1.595	0.570	7.823	0.005	4.929

	Distance (2)	0.000	0.610	0.000	1.000	1.000
	Constant	-1.190	0.432	7.594	0.006	0.304

Figure legends:

Figure 1. Map of the western Serengeti showing some villages where the meat taste were conducted.

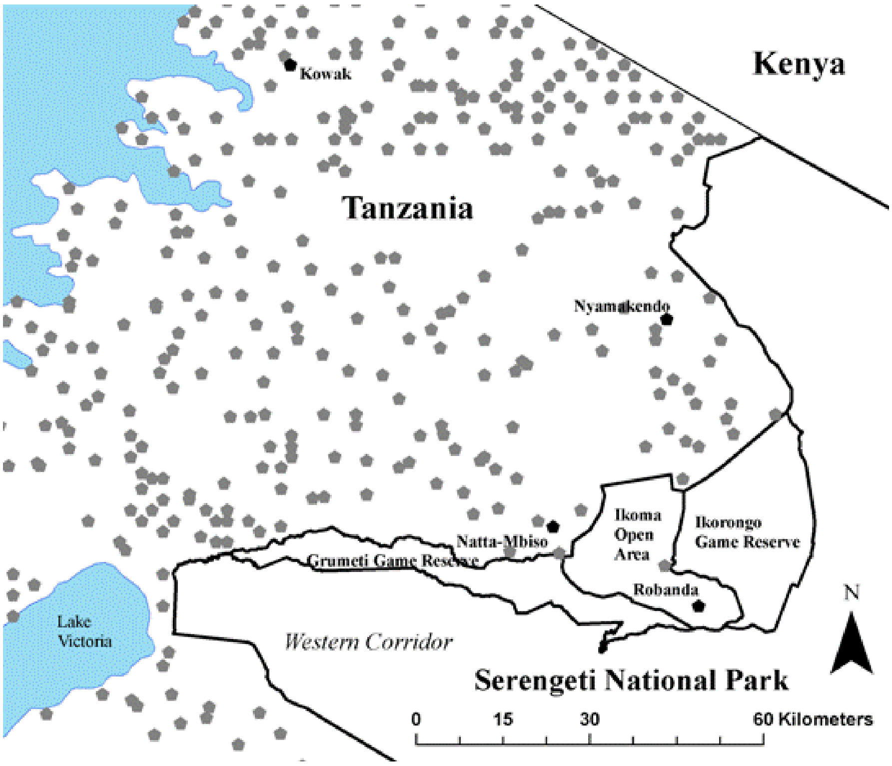
Kenya
Kowak
Tanzania
Nyamakendo
Ikoma
Open
Area
Ikorongo
Game Reserve
Natta-Mbiso
Grumeti Game Reserve
Robanda
N
Lake
Victoria
Western Corridor
Serengeti National Park
0
15
30
60 Kilometers

Figure 1.

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus.*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus*.

1987	Jarle Inge Holten	Dr. philos Bothany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).
1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.
1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants

1991	Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
1991	Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992	Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek.
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*.
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers

1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
1994	Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995	Hanne Christensen	Dr. scient. Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
1995	Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
1995	Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995	Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden.
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996	Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
1996	Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996	Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.
1996	Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae.
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.

1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997	Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.
1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.
1998	Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)

1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999	Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard

2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*

2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius

2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Ander Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	Phd Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	phD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	phD Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	phD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	phD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	phD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	phD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	phD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	phD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	phD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation

2007	Kari Jørgensen	phD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	phD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, */Mamestra Brassicae/* L. (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	phD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	phD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	phD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania