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Preface

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This thesis is based on the following papers:

- I** Holmern, T., Nyahongo, J., Røskaft, E., 2007. Livestock loss caused by predators outside the Serengeti National Park, Tanzania. *Biological Conservation* 135: 534-542.
- II** Holmern, T., Mkama, S.Y., Muya, J., Røskaft, E., 2006. Intraspecific prey choice of bushmeat hunters outside the Serengeti National Park, Tanzania: a preliminary analysis. *African Zoology* 41: 81-87.
- III** Setsaas, T.H., Holmern, T., Mwakalebe, G., Stokke, S., Røskaft, E., 2007. How does human exploitation affect impala populations in protected and partially protected areas? – A case study from the Serengeti Ecosystem, Tanzania. *Biological Conservation* 136: 563-570.
- IV** Holmern, T., Setsaas, T.H., Melis, C., Røskaft, E., (manuscript) Margins of safety and escape responses in Thomson's gazelle.
- V** Holmern, T., Røskaft, E., Mbaruka, J.Y., Mkama, S.Y., Muya, J., 2002. Uneconomical game cropping in a community-based conservation program outside the Serengeti National Park, Tanzania. *Oryx* 36: 364-372.
- VI** Holmern, T., Muya, J., Røskaft, E., 2007. Local law enforcement and illegal bushmeat hunting outside the Serengeti National Park, Tanzania. *Environmental Conservation* 34: 55-63.

Declaration of contribution

ER contributed with ideas, planning of fieldwork, data collection and commenting on the ms throughout. Contribution of other co-authors: Paper I, JN commented on the ms; Paper II, SYM and JM participated, helped in planning the fieldwork and commented on the ms; Paper III, Planning and data collection was done together with THS, GM and SS. I did part of the data analysis. GM, SS and myself commented on the ms; Paper IV, data collection was done together with THS, ER and CM. THS and CM commented the ms; Paper V, JYM, SYM and JM participated, helped in planning the fieldwork and commented on the ms; Paper VI, JM helped in planning the fieldwork and commented on the ms.

Summary

Bushmeat hunting is identified as the major threat to wildlife in sub-Saharan Africa. The trade which includes both rural and urban dwellers is linked to deforestation, and especially the development of roads, which has increased human settlements and provided access to improved transport of animal products. Demand from a burgeoning human population is adding to the unsustainability of the activity. Many wildlife populations in East and Southern Africa have already experienced dramatic declines and range contractions because of illegal hunting. Conservation efforts have largely been directed along two approaches: establishing protected areas and including local people in the management of wildlife, while sharing wildlife related benefits. However, both strict protected areas, such as national parks, and partially protected areas have not by themselves been able to improve the situation. Moreover, laws and regulations, together with law enforcement have also been unsuccessful at reducing illegal activities.

Community-based conservation (CBC) was introduced in recognition of the importance of including local people and partially and unprotected areas as part of wildlife management in the wider landscape context. This has been a widely adopted approach in East and Southern Africa, and Tanzania has also invested considerable efforts to use CBC and buffer zone areas (i.e. partially protected areas) in order to create incentives for conservation and for alleviating poverty. In the Serengeti ecosystem, illegal bushmeat hunting is identified as the top-most threat to wildlife populations. At the same time, local people bear substantial costs from having large wildlife as neighbours, which cause conflicts and resentment towards protected areas. In the mid 1980s the Tanzanian government established Serengeti Regional Conservation Project (SRCP) as one of the first CBCs in the country to tackle the problems experienced in the ecosystem, and in particular that of the western Serengeti, where encroachment and illegal hunting were most severe. However, despite its potential importance little information has been available for evaluating its effect.

This thesis focuses on the performance of wildlife conservation efforts in partially protected areas by using the western section of the Serengeti ecosystem in Tanzania as a case study. The thesis first explores some of the costs and benefits for local people that are associated with wildlife, and the effects of human disturbance on wildlife, then it evaluates some of the efforts implemented to include local people in conservation and to curb illegal activities.

The conflict between large predators and people epitomises the struggle of conservation. Local people in the western Serengeti suffer high costs due to livestock loss

from large predators and this effect extends relatively far into human settled areas. Not surprisingly, retaliatory killing is widely accepted. Education seemed to reduce the acceptance of killing, and for livestock keepers the perceived effectiveness of livestock protection measures, as well as the number of livestock loss influenced attitudes. Thus, in order to reduce the effect of retaliatory killings on predator populations in the Serengeti, it is vital to improve protection measures for livestock and offer local people improved education, which will also provide them easier access to alternative livelihoods.

In accordance with previous studies, illegal bushmeat hunting was widespread in the area outside the Serengeti National Park, both from SRCP and non-project villages. There was also a temporal variation in hunting efforts which increased when the wildebeest (*Connochaetes taurinus*) migration travelled through the area. The majority of the harvest was represented by migratory herbivores, but also resident herbivores were targeted. Males were exposed to a higher risk of being killed, probably due to behavioural differences between the sexes, rather than as a result of the hunter's prey choice. The main reason for hunting was subsistence, although some also had commercial motives. Illegal bushmeat hunting reduced impala (*Aepyceros melampus*) density, especially in the partially protected areas, as well as probably causing a more female biased sex ratio. In addition, animals became more wary in the areas under high hunting pressure, which indicates that demography and behaviour can be used as indicators of human exploitation. Animals, like Thomson's gazelle (*Gazella thomsoni*), appeared not to monitor the expected time a predator would take to reach their location, but instead relied only on distance as a cue to assess when to flee.

The game cropping operation (the commercial utilisation of wild animal populations in natural habitats) of SRCP was economically unsustainable. The expected revenue per villager from the cropping program was low compared to the value of the potential income generated by illegal bushmeat hunting. In addition, the degree of participation in wildlife management was also restricted. One underlying condition for conservation to take place when including local people in benefit sharing, is that communities must be able to reduce threats to biodiversity themselves – that is they must have some control over the area, and can enforce policies to reduce threats through their own activities. Local law enforcement in the project villages showed substantial efforts in curbing illegal activities inside their patrol areas. However, project villages that derived higher benefit levels were more zealous in executing their authority. District level units had a low influence on the probability of making arrests, which suggests that measures must be taken to increase the resources available for enforcement, as well as increasing collaboration, in order to reduce illegal activities.

Introduction

The mounting pressure from Africa's human population is threatening the continent's amazing biodiversity. The co-occurrence of high vertebrate species richness and high human densities are also worrying, suggesting that substantial human induced environmental changes are likely to continue (Cincotta et al. 2000; Balmford et al. 2001). However, species extinction is only the end product of a gradual depletion of biodiversity. Today, the population sizes of many wildlife species are either experiencing severe reductions or species have become locally extinct due to human related activities (Edroma and Kenyi 1985; Dublin et al. 1990; Milner-Gulland and Leader-Williams 1992; FitzGibbon et al. 1995; Caro et al. 1998; Barnett 2000; Brashares et al. 2004). Local or ecological extinction may lead to a cascading effect in the ecosystem (Naiman 1988; Hobbs 1996; Sinclair et al. 2003; Ripple and Beschta 2004; Augustine and McNaughton 2006) that may ultimately cause disruption to ecosystem functioning (Lyons et al. 2005).

Most rural people in sub-Saharan Africa are agropastoral, combining small-scale farming with livestock keeping, or specialise in herding (pastoralists) or farming. Their reliance on natural resources (i.e. water, firewood, rangeland for livestock, fish and bushmeat) for sustenance means that exhaustion of their resource base has not only serious implications for conservation, but also for human welfare.

Protected areas

Two major strategies have been employed to reduce the loss of biodiversity: establishing protected areas, and allowing local people to benefit economically from wildlife, thus creating an incentive to counter threats (i.e. community based conservation initiatives). Historically the most common strategy for conserving biodiversity is the establishment of protected areas, thereby restricting human activities (Table 1). The number of protected areas has increased rapidly in the past century, reaching a total coverage of the land area of 12% or over 20 million km² in 2005 (Chape et al. 2005). The growth has particularly been pronounced in developing countries where biodiversity is greatest (Naughton-Treves et al. 2005).

In East and Southern Africa many of the large well-known protected areas were first established during the colonial period for trophy hunting or for their aesthetic value (Neumann 1998, 2002). For example, in Tanzania, a small section of the Serengeti National Park was already gazetted as a partial Game Reserve in 1921, and later in 1929 as a full Game Reserve. Another renown National Park, the Kruger, in South Africa was also established in

the same period (Mabunda et al. 2003). The colonial rulers emphasised nature preservation according to an Anglo-American ideal, where humans were not regarded as a part of the ecosystem, despite the fact that most of tropical Africa was occupied and used by local tribes (Blaut 1993; Neumann 1998). Consequently, the establishment of protected areas and later the eviction of local people created fertile grounds for antagonism and conflict. After independence African governments followed in the footsteps of the colonial rulers, realising the economic potential of wildlife tourism, and partly because of active encouragement by foreign non-governmental organisations and development agencies (Bonner 1993; Levine 2002; Chapin 2004). Gradually many of the past reserves were upgraded to Game Reserves and National Parks, thus banning all forms of consumptive activities by local people, and emphasis was put on law enforcement to curb illegal activities. The result was that rural communities became marginalised, alienated from both their traditional natural resources and their governments, with few options to offset the costs of wildlife protection, in the face of what has later been termed “fortress conservation” (Neumann 1998).

Effects of human activities on wildlife

Numerous protected areas have been established, but many species are still going extinct and the loss of natural habitat is high. Protected areas face a diverse array of both internal and external threats that continue to cause loss of biodiversity. Some threats come from afar, such as air pollution, alien species and large dam construction (Cole and Landres 1996; Gereta

Table 1. IUCN protected area categories (UNEP-WCMC 2005).

Type	Category	Description
Strict protected areas	Ia Strict Nature Reserve	Protected area managed for science
	Ib Wilderness Area	Protected area managed mainly for wilderness protection
	II National Park	Protected area managed mainly for ecosystem protection and recreation
	III Natural Monument	Protected area managed mainly for conservation of specific natural features
Partially protected areas	IV Habitat / Species Management Area	Protected area managed mainly for conservation through management intervention
	V Protected Landscape / Seascape	Protected area managed mainly for landscape/seascape conservation and recreation
	VI Managed Resource Protected Area	Protected area managed mainly for the sustainable use of natural ecosystems

2004; Foxcroft et al. 2006), and are thus beyond the direct influence of protected area management. But the more important impacts on many protected areas are caused by human encroachment and the increase in human activities that are associated with human settlements and infrastructures (Campbell and Hofer 1995; Drews 1995; Hofer et al. 1996; Wilkie and Carpenter 1999; Pelkey et al. 2000).

In East and Southern Africa widespread illegal hunting and deforestation are identified as the major threats to wildlife (Dublin and Douglas-Hamilton 1987; Hofer et al. 1996; Barnett 2000; Pelkey et al. 2000). For example, low levels of law enforcement and high profit margins for illegal trophy hunting caused populations of key species, such as black rhino (*Diceros bicornis*) and elephant (*Loxodonta africana*), in East Africa to plummet during the 1970s and 1980s (Dublin and Douglas-Hamilton 1987; Barnes and Kampela 1991; Milner-Gulland and Leader-Williams 1992; Stiles 2004). The trade in wild animal meat, or bushmeat, is also causing striking declines in other wildlife populations (Edroma and Kenyi 1985; Dublin et al. 1990; Campbell and Borner 1995; FitzGibbon et al. 1995; Caro et al. 1998; Barnett 2000; Nielsen 2005), as elsewhere in sub-Saharan Africa (Wilkie and Carpenter 1999; Brashares et al. 2004). In Tanzania, partially protected areas (IUCN category \leq IV) appear to be particularly hard-hit by illegal bushmeat hunting (Caro et al. 1998, 1999a), combined with high rates of habitat degradation (Pelkey et al. 2000). In the past, hunting was mainly carried out for subsistence reasons, but in recent years illegal bushmeat hunting has increased dramatically for several reasons; increases in human populations (Africa's population increased from 224 million in 1950 to 960 million in 2005), improved infrastructure which facilitates transport of and access to wildlife, the use of efficient modern hunting technologies (i.e. firearms and wire snares), loss of traditional hunting controls (i.e. taboos, avoidance of certain age and sex categories) and greatly increased commercialisation of hunting (Campbell and Hofer 1995; Hofer et al. 1996; Wilkie and Carpenter 1999; du Toit 2002; UN 2005). However, the concept of the "ecologically noble savage", that shows self-control in order not to over-exploit vulnerable species, has been put in doubt (Alvard 1993).

Human disturbance may also manifest itself through more indirect effects on wildlife. Human settlements inside partially protected areas invariably lead to expansions of settlements as the population increases and to a pressure for land uses that are not compatible with wildlife (i.e. agriculture, small scale mining) (Homewood et al. 2001). Wildlife will therefore be forced to utilise other potentially sub-optimal areas, since many human activities compete directly with wildlife for areas with high productivity (Ottichillo et al. 2001). Moreover, a number of studies document that livestock grazing, which is often allowed in

partially protected areas, causes changes in the composition and structure of the vegetation (Tobler et al. 2003), competes with wildlife for forage (Voeten and Prins 1999; Madhusudan 2004), and may cause displacement of megaherbivores which has large consequences for long-term changes in ecosystem structure and function (du Toit and Cummings 1999; Skarpe et al. 2004). Transmission of diseases between livestock and wildlife (e.g. rinderpest, tuberculosis) or between domestic dogs and carnivores (e.g. rabies, canine distemper) is also a recurrent problem (Dobson 1995; Packer et al. 1999).

Vulnerability of wildlife to disturbance depends both on exposure to anthropogenic threats, as well as biological traits that may make some species more threatened with extinction than others. Biomass and gestation length are traits that are positively associated with an increased extinction risk (Cardillo et al. 2005), but also behavioural traits have been implicated in increasing the vulnerability for some species. For example, larger bodied species are more wary (i.e. less risk tolerant), and initiate flight at greater distances than smaller species (Blumstein 2006). High hunting pressure or other types of disturbance may therefore be especially costly to large species. Greater wariness and use of more protected habitat could have negative effects on food intake rates and exposure to predation, thus ultimately affecting recruitment rates (Sinclair and Arcese 1995a; Kilgo et al. 1998; Blumstein et al. 2005).

Local participation and benefit sharing

Protected areas are vital for safeguarding species, but conservation solely through a protectionist approach has obvious weaknesses. Apart from having relatively high economic costs (Leader-Williams and Albon 1988; Jachmann and Billiow 1997), protected areas have a low economic return compared with other human land uses (Norton-Griffiths 1996), fail to incorporate a perspective that stretches into the wider unprotected landscape (Newmark 1996; Ottichilo et al. 2001; Gereta 2004), and exclusion of indigenous and local people from vital natural resources create hostility and loss of public support (Newmark et al. 1993; Neumann 1998; Kidegesho et al. 2006). In addition, Rodriguez et al. (2004) reported that the global protected area coverage of vertebrate species is currently insufficient, since 12 % of vertebrate species are not protected in any part of their range.

During the 1980s initiatives that attempted to integrate the interests and needs of local people with conservation were therefore seen as a possible complementary approach. These initiatives target buffer zones and other parts of the human dominated habitats, and have been termed Integrated Community and Development Projects (ICDP), Community Conservation

(CC), Community-based natural resource management (CBNRM) or Community based conservation (CBC)¹. CBC initiatives' key assumption is that distribution of benefits will make local people motivated to comply with restrictions on use of natural resources (Hackel 1999; Newmark and Hough 2002; Salafsky et al. 2002). The three main areas in which CBC is being applied are in wildlife, forestry and marine management, whereas in East and Southern Africa the majority of projects centre on wildlife (Lewis et al. 1990; Child 1996; Songorwa 1999; Barnes et al. 2002, but see McClanahan et al. 2005 for an example of marine management). CBC activities primarily focus on: 1) protected area management, 2) establishment of “buffer zones” where low impact human activities are allowed, and 3) local social and economic development (Wells and Brandon 1993). Buffer zones, such as partially protected areas, compose the majority of Africa’s protected areas (70.7 % of those assigned to IUCN categories), and are both important for conservation of biodiversity and have a considerable potential for CBC initiatives. For example, Tanzania, which have set aside an impressive 39.6 % of its land area as protected areas, where partially protected areas form the majority (Figure 1, Table 2) (UNEP-WCMC 2005).

Table 2. The percentage (and km²) of total land area covered by protected areas for countries in East and Southern Africa, where the area coverage is given by the IUCN category and as a percent of the total PA coverage. Includes IUCN categories I-VI and areas termed as “other” (i.e. protected areas not classified by IUCN)*. Marine and littoral protected areas are not included (WRI 2005).

Country	Percent total land area (km ²)	IUCN category		
		I-II	III-V	VI and “other”
Namibia	5.6 (46,000)	68.7%	1.2%	30.1%
Mozambique	5.7 (45,300)	34.8%	37.7%	27.5%
South Africa	6.2 (75,630)	53.2%	34.0%	12.8%
Angola	10 (125,480)	23.6%	18.4%	58.0%
Kenya	12.4 (71,940)	47.7%	0.7%	51.6%
Zimbabwe	14.7 (57,520)	47.2%	6.7%	46.1%
Malawi	16.4 (19,410)	35.9%	18.7%	45.4%
Uganda	26.7 (64,270)	11.9%	15.5%	72.6%
Botswana	30.1 (174,920)	26.0%	34.0%	40.0%
Tanzania	39.6 (374,280)	10.9%	25.9%	63.2%
Zambia	41.5 (312,250)	20.4%	0.02%	79.6%

*Tanzania’s protected areas fall into the following IUCN categories: II=National Parks, IV=Game Reserves, VI=Ngorongoro Conservation Area, Game Controlled Areas and “other”=Forest Reserves (Open Areas are thus not included in the table).

¹ The term Community-based conservation (CBC) as used here has broadly the same meaning as Community-based natural resource management (CBNRM). Often the CBC is assumed to also involve the utilisation of larger species of wild animals, while the CBNRM is associated with the management/utilisation of all natural resources within an area.

CBC has been especially fashionable among development agencies (Chapin 2004). The incorporation of partially protected areas into rural poverty reduction strategies is also strongly advocated by the IUCN's conservation policy (Phillips 1999; Mulongoy and Chape 2004).

According to Alpert (1996) over a 100 of these projects have been described, including more than 50 in at least 20 countries of sub-Saharan Africa. Probably the most famous CBC initiatives have been the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) in Zimbabwe and the Administrative Management Design for Game Management Areas (ADMADe) in Zambia. Both programs involve rural people living on communal lands or close to protected areas in the sustainable use of natural resources. The economic benefits generated are to a large degree based on revenues from trophy hunting and live sales of wild animals (Child 1996; Lewis and Alpert 1997).

Similarly, Tanzania has incorporated CBC as part of its conservation strategy, and started a number of projects, such as the Community Conservation Services (CCS) of Tanzania National Parks (TANAPA), the Selous Conservation Program (SCP), Matumizi Bora ya Malihai Idodi na Pawaga (MBOMIPA) in Ruaha and Serengeti Regional Conservation Project (SRCP) (Mbanjo et al. 1995; Songorwa 1999; Baldus and Cauldwell 2004). However, inclusion of local people has long traditions in Tanzania, where the Ngorongoro Conservation Area was already in 1959 established as a multiple use area. The more participatory of the CBC initiatives, have progressively devolved responsibility for wildlife on village land to local people, through establishment of tenure and legal rights to wildlife (URT 2004; Walsh 2000). Different forms of sustainable use of wildlife have gradually been applied, ranging from community hunting of assigned quotas to public auctioning of village hunting quotas. Establishment of Wildlife Management Area, which is a new protected area category in Tanzania that is intended to be managed by local villages, is also a crucial part of these projects (Baldus and Cauldwell 2004; Paper VI). Capacity building and strengthening of village management institutions are also part of the activities (Mbanjo et al. 1995; Songorwa 1999; Walsh 2000). In comparison, the CCS approach only uses parts of park revenues to finance community facilities (i.e. schools, dispensaries) in villages adjacent to the National Parks.

The return of “fortress conservation”?

Regardless of considerable investments, interest and hope vested in CBCs by the conservation community, the results have been somewhat equivocal, but the successes are often isolated

and subsidised by donors (Newmark and Hough 2000; Salafsky et al. 2001). The reasons why CBCs have been unable to stem or reverse the negative trends for wildlife have been widely debated (Kiss 1990; Wells and Brandon 1993; Barrett and Arcese 1995; Gibson and Marks 1995; Alpert 1996; Hackel 1999; Lewis and Phiri 1998; Songorwa 1999; Newmark and Hough 2000; Adams and Hulme 2001). Some of the main points to come out of this debate are that: first, the implementation often has design problems, such as unattainable objectives, inadequate capacity (project staff and villages), lack of baseline research, being top-down initiated and donor dependent (Kremen et al. 1994; Newmark and Hough 2000). Second, wildlife related benefits are usually too small to offset costs (i.e. wildlife damage, income costs of reducing illegal hunting), and economic development is often poorly linked to conservation (Kiss 1990; Wells and Brandon 1993; Lewis and Phiri 1998; Paper V). Moreover, elite capture is a recurrent problem and reinforces existing intra-village power structures instead of alleviating the livelihood of the poorest, which often have no alternative than illegal resource exploitation. Third, a central assumption is that when local communities receive some direct benefit, they will have the incentive to conserve those areas, and will take action to do so. According to Salafsky et al. (2001) several factors need to be

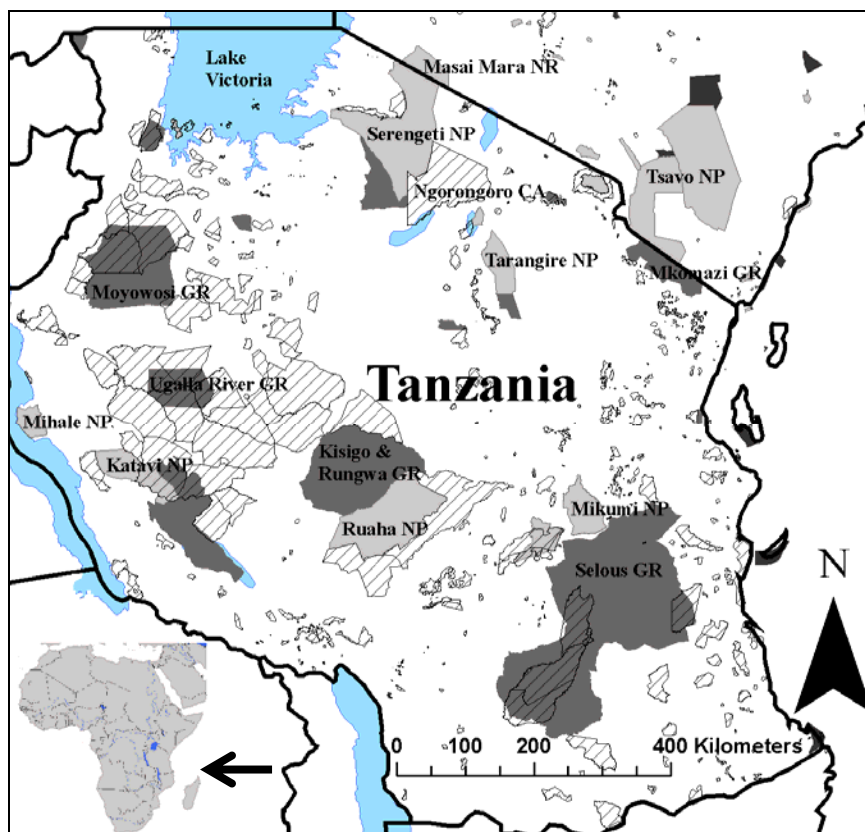


Figure 1. Map showing the distribution of the different protected areas in Tanzania. Light grey areas are National Parks (NP), dark grey areas are Game Reserves (GR) and hatched areas are Game Controlled Areas, Forest Reserves, Open Areas and “other” partially protected areas. Inset map shows the location of Tanzania (UNEP-WCMC 2005).

fulfilled for this to happen, and one key issue is that communities must be able to reduce threats through their own activities. There is considerable evidence that policing is crucial to curtail illegal activities (Leader-Williams and Albon 1988; Leader-Williams et al. 1990; Hilborn et al. 2006) and can, depending on the threats, also in some instances effectively take place through traditional regulations (Berkes 2004), or through local law enforcement units (Lewis et al. 1990; Paper VI). But adequate mechanisms for control is often lacking in CBC initiatives (Kiss 1990). Fourth, a few studies are critical to the sustainable use philosophy that CBCs emphasise through linking wildlife harvesting and human development (Barrett and Arcese 1995; Newmark and Hough 2000). Lastly, in the same way as protected areas, CBCs cannot counter external threats. Especially political stability is a prerequisite for a viable tourism industry. Nevertheless, some segments of the tourism industry, like trophy hunting, are relatively resilient to political turmoil (Lindsey et al. 2006).

Despite these pitfalls and shortcomings, there are projects that have reported some substantial achievements (Lewis et al. 1990; Walsh 2000; Salafsky et al. 2001; Barnes and MacGregor 2002; Kidegesho et al. 2006), but it might still be too early to place judgement on these projects since they require a long term perspective (Adams and Hulme 2001). But some of the required conditions identified for CBCs to work are among others: abundant wildlife resource (preferable of trophy species), low human population density and interest of the local community (Child 1996; Songorwa 1999). Yet, since many CBCs currently have not been able to deliver as expected, there has been a number of studies that have suggested the necessity for a return to enforcement and exclusion of human activities from protected areas in order to protect wildlife (Spinage 1998; Terborgh 1999).

Aims for the thesis

The thesis evaluates the performance of wildlife conservation in partially protected areas by using the western section of the Serengeti ecosystem in Tanzania as a case study. The first part of this thesis (Papers I-IV) focuses on costs and benefits of wildlife, as well as the consequences of human exploitation on wildlife, whereas the second part (Papers V-VI) evaluates strategies that have been employed to reduce some of the negative impacts of human disturbance.

Methods

Study area

The study area is located in the north-eastern corner of Tanzania (Figure 1) on the north-western side of the Serengeti National Park (14,763 km²). The Serengeti National Park gazetted in 1951 is the largest National Park in Tanzania and is both a world heritage site, and forms together with the Ngorongoro Conservation Area, a Biosphere Reserve (established in 1981) (Figure 2 and 3). A number of partially protected areas border the western corridor of the Serengeti National Park, which stretches westwards towards the beaches of Speke Gulf in Lake Victoria. The regulations for the Serengeti National Park permits no human settlement or extraction of natural resources. However, the neighbouring partially protected areas, such as Ikorongo and Grumeti Game Reserves, allow trophy hunting and game cropping. The Ikoma Open Area allows limited cattle grazing, firewood collection, hunting (game cropping, resident and trophy hunting) and bee keeping. The Serengeti ecosystem harbours one of the worlds last remaining large scale ungulate migrations. The migration of 1.3 million wildebeest (*Connochaetes taurinus*), and 0.6 million zebra (*Equus burchelli*) and gazelles (*Gazella thomsoni* and *G. granti*) follows a rainfall and grass productivity gradient on their annual migration cycle (Boone et al. 2006). During the dry season, parts of the wildebeest migration utilise the partially protected areas (i.e. Ikorongo GR, Grumeti GR, Ikoma OA) on

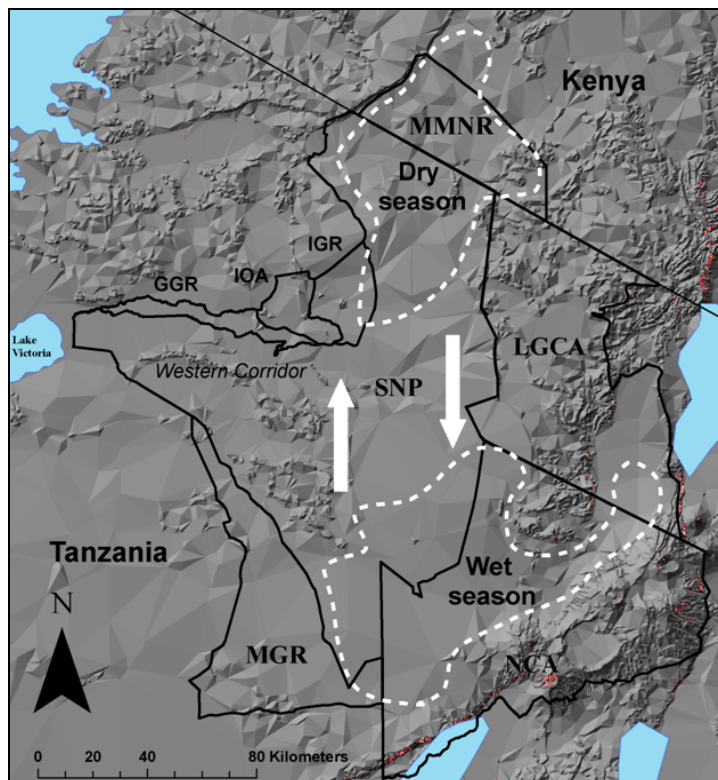


Figure 2. Map over the Serengeti Ecosystem. Areas include Serengeti National Park (SNP), Loliondo Game Controlled Area (LGCA), Ngorongoro Conservation Area (NCA), Maswa Game Reserve (MGR), Grumeti Game Reserve (GGR), Ikoma Open Area (IOA), Ikorongo Game Reserve (IGR) and Masai Mara National Reserve (MMNR) in Kenya. The wildebeest are in southern part during the wet season (Dec-May), when the calving takes place, and the northern part during the dry season (Aug-Nov). On their northward migration (May-Jul), the wildebeest herds use parts of the Western Corridor, as well as the adjacent partially and non-protected areas, depending upon the rainfall pattern (adapted from Thirgood et al. 2004 and Rusch et al. 2005).



Figure 3. Adjacent to the north-eastern border of the Ngorongoro Conservation Area towers the active volcano Ol Doinyo Lengai (2890 m). The soil on the Serengeti plains originates from ashes from the many volcanoes in the area. The Rift Valley escarpment can be seen in the background (Photo: T. Holmern).

their way north towards Masai Mara National Reserve in Kenya (Thirgood et al. 2004; Rusch et al. 2005). The ecosystem, and in particular the western corridor, also contains large concentrations of resident herbivores that do not migrate, such as, giraffe (*Giraffa camelopardalis*), buffalo (*Syncerus caffer*), topi (*Damiliscus korrigum*), impala (*Aepyceros melampus*) and warthog (*Phacochoerus aethiopicus*) (Figure 4). These large concentrations of herbivores sustain a diverse array of predators.

There is a high human population density in the western Serengeti (> 70 people/km², human population in Mara Region >1.3 million), where the villages are multiethnic, large (>1500 inhabitants) and have an annual population growth rate of approximately 2.9% (Figure 5) (URT 2002). There is a high diversity of tribes, mainly of Bantu origin. The majority of the people in the study area are very poor subsistence farmers (average annual cash income of US \$ 140 in 2001) (Borge 2003), complementing in a varying degree with livestock keeping and small-scale trade. Food crops include maize, cassava, millet and sorghum, while some grow cotton as a cash crop. The crop cycle follows the rain-pattern and usually the crops are planted twice a year, with planting in February and August-October, harvesting in June and January respectively. Cattle, goats, sheep and donkeys are the most common livestock kept. The areas immediately adjoining the protected areas (< 10 km) are also experiencing a high immigration rate (Campbell and Hofer 1995). Moreover, many rural inhabitants rely heavily on bushmeat protein supply and the potential it provides for generating cash incomes (Barnett 2000; Loibooki et al. 2002; Paper V)



Figure 4. The savannah and acacia woodlands are typical for the central ranges of the Serengeti. The western corridor lies beyond Nyaraswiga and Kubu Kubu Hills that can be seen in the background (Photo: T. Holmern).

Illegal hunting

Hunting has been an integral part of life in the Serengeti for centuries. Illegal hunting mainly originates from the villages in the west of the Serengeti National Park, since the pastoralist Maasai living to the east solely live on livestock and do not eat wild animal meat. However, the rapid human population growth and the commercialisation of illegal hunting have caused considerable concern over the sustainability of the harvest (Campbell and Borner 1995; Campbell and Hofer 1995; Hofer et al. 1996). The most common hunting method is the use of wire snares, but also more active methods are used (Arcese et al. 1995; Paper II). Illegal commercial hunting has earlier had severe impact on both the elephant and the buffalo populations in the northern and western Serengeti (Dublin and Douglas-Hamilton 1987; Dublin et al. 1990) and made the black rhino population crash from an approximate size of 1000 in 1975 to local extinction in the early 1980s (Hilborn et al. 2006). Especially giraffe, buffalo, impala and topi, that have a habitat preference for woodlands and thickets, are disproportionately caught since snares are usually set in thickets (Arcese et al. 1995). Although resident herbivores only constitute a minor part of the offtake compared to migratory herbivores, illegal hunting of resident wildlife is profitable in 68% of the area (Hofer et al. 2000). However, for the most abundant migratory species, the wildebeest, offtake appears to be within sustainable limits (Mduma et al. 1998), although there is some disagreement on the harvest level (Campbell and Hofer 1995; Hofer et al. 1996). The total harvest of ungulates has been estimated to approximately 160,000 animals (70% of the harvest is migratory herbivores) and to benefit 1 million people (Hofer et al. 1996). Herbivores are usually the target prey for hunters, but snare hunting also has serious impact on non-target species, such as spotted hyena (*Crocuta crocuta*) (Hofer et al. 1993).

Community-based conservation

The western Serengeti was one of the first areas in Tanzania to be targeted for a CBC, because of increasing problems with illegal hunting and human encroachment (Mbano et al. 1995). Currently, in the north-western Serengeti, there are two CBC initiatives that work with the villages adjacent to the National Park, the CCS and SRCP. CCS started out in 1994 and funds the construction of communal facilities, but has no involvement in capacity building or wildlife management. On the other hand, SRCP was created in 1985 and has actively been collaborating with the villages around the National Park, although its main focus has been the villages bordering the western corridor (SRCP 1999). SRCP has since 1993 provided legal game meat through a game cropping operation (the commercial utilisation of wild animal populations in natural habitats), together with providing capacity and institutional building, as well as different extension services (Mbano et al. 1995; Paper V).

Study species

The main large carnivore species in the Serengeti ecosystem are spotted hyenas, lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*), but also smaller carnivores like the jackals (*Canis mesomelas*, *C. adustus*, *C. aureus*) are found throughout the ecosystem (Table 3). However, spotted hyenas and lions account for approximately 85% of the predation on large herbivores in the Serengeti. Much of the prey base for the larger carnivores during parts of the year is made up of the migratory herds. But during the periods where these species are unavailable, other resident prey becomes important parts of the diet (Kruuk 1972; Schaller 1972). The availability of resident prey has been suggested as the limiting factor for predators holding territories (Fryxell et al. 1988), although other reasons such as patterns of prey choice and social factors may play a role (Hofer and East 1995). However, the spotted hyena, because of its ability to travel large distances (i.e. commuting) in search for migratory prey and because of their social system which allows commuters to pass through neighbouring territories, are less dependent on resident herbivores. These adaptations probably have contributed to the large number of spotted hyenas in the ecosystem (Hofer and East 1995; Mills and Hofer 1998).

Table 3. Characteristics of some of the predators found in the Serengeti National Park and adjoining partially protected areas (partly adapted after Hofer and East 1995).

Species	Population size	Body size	Territory size	Social structure	Movements	Activity pattern	Principal natural prey	Livestock at highest risk
Spotted hyena	5200 - 6000	55 – 85 kg	9 – 56 km ²	Large social groups / solitary	Commuting system (follow migratory prey outside territories)	Day and night	Wildebeest, Thomson's gazelle, zebra	Sheep, goats, donkeys & cattle
Lion	2500	120 – 200 kg	20 – 300 km ²	Large social groups / solitary	Mainly restricted to territories, but may follow migratory prey outside	Day and night	Wildebeest, zebra, buffalo, Thomson's gazelle	Sheep, goats, donkeys & cattle
Leopard	1000	35 – 85 kg	♀: 14 - 60 km ² , ♂: ca. 60 km ²	Solitary	Mainly restricted to territories	Mainly night	Impala, Thomson's gazelle, dik dik, reedbuck	Sheep, goats, donkeys & cattle
Cheetah	250	40 – 60 kg	800 - 1500 km ²	Solitary	Following movements of principal prey	Day	Thomson's gazelle, Grant gazelle, impala	Sheep & goats
African wild dog	< 30*	18 – 28 kg	1500 - 2000 km ²	Large social groups	Follows movement of principal prey	Day	Thomson's gazelle, wildebeest, zebra	Sheep, goats, donkeys & cattle
Black-backed jackal	6300	6.5 – 10 kg	< 20 km ²	Small social groups	Mainly restricted to territories	Day and night	Small mammals, but also fawns of gazelles	Sheep & goats
Golden jackal	Not available	6 – 10 kg	< 20 km ²	Small social groups	Mainly restricted to territories	Day and night	Small mammals, but also fawns of gazelles	Sheep & goats
Side striped jackal	Not available	6 – 13.5 kg	< 20 km ²	Small social groups	Mainly restricted to territories	Day and night	Small mammals, but also fawns of gazelles	Sheep & goats
Baboon	Not available	10-30 kg	2-30 km ²	Large social groups	Mainly restricted to territories	Day	Plants, fruit, insects, small mammals, fawns of gazelles	Sheep & goats

References: Populations size: Mills and Hofer 1998, Packer 1990, Schaller 1972, Gros 2002, *Pers com. R. Fyumagwa, Caro and Durant 1995; Body size: Haltenorth and Diller 1996; Territory size: Höner et al. 2005, Handby and Bygott 1979, Bertram 1982, Caro 1994; Frame et al. 1979, Haltenorth and Diller 1996; Social status: Haltenorth and Diller 1996; Movement: Mills and Hofer 1997, Haltenorth and Diller 1996; Activity pattern: Haltenorth and Diller 1996; Estes 1990; Principal natural prey: Kruuk 1972, Schaller 1972, Bertram 1979; Haltenorth and Diller 1996; Livestock: Kruuk 1980; Rasmussen 1999; Butler 2000; Patterson et al. 2004; Paper I.



Figure 5. Villages consist of widely dispersed households where living quarters and enclosures for livestock are located on the same compound. The picture to the right illustrates a typical hut used for keeping sheep and goats at night (Photo: T. Holmern).

The two main antelope species included in this thesis are impala and Thomson's gazelle. Impala is a medium sized antelope (40 kg), commonly occurring in the semi-arid and bush savannas of southern Africa (Haltenorth and Diller 1996; Estes 1990). It is a highly social species in which the females range in medium to large groups, with each group accompanied by an adult male (Murray 1982). As in many other polygynous antelope species (Jarman 1974), males carry horns whereas females are hornless. In the Serengeti National Park it is one of the most numerous non-migrating herbivores (population size of 80,000 in 1995), and it is mainly found in the extensive woodlands to the north and west (Campbell and Hofer 1995).

The Thomson's gazelle is a small grazer of about 20 kg (Haltenorth and Diller 1996), which is found in an isolated population in southern Sudan, as well as from northern Tanzania to northern Kenya (Estes 1990). It is associated with the grasslands and in Serengeti large herds congregate on the short grass plains during December – February (approximately 330,000 individuals in 1991) (Campbell and Borner 1995). In the dry period (June – October) it migrates westward, partly following the migration of wildebeest and zebra (Maddock 1979). Male gazelles are territorial throughout their adult lives, but during the non-territorial periods males usually spend their time in bachelor groups or as part of a mixed herd. Both males and females carry horns, although females have only short spikes.

Data collection

Data for this thesis was collected during several field periods. Data on illegal bushmeat hunting was principally collected during 1998 – 1999 by collaborating with local law enforcement units, which were employed by the villages' part of SRCP (Paper II, V and VI).

During the dry season of 2003 we collected the data used for the density estimates of impala, by means of transects in the different protected areas. Parallel to this study we conducted the flight response trials of impala, as well as Thomson's gazelle (Paper III and IV). In 2004 we also conducted a questionnaire survey in seven of the villages in the western Serengeti, where we, among other things, assessed conflict levels with large predators (Paper I). For more complete descriptions of methods see the respective papers.

Main results

Human – wildlife conflicts (Paper I)

Human – wildlife conflicts can seriously affect the relationship with adjacent protected areas. Here I examine livestock depredation which is a key conflict, and ask the question: what is the level of livestock depredation in the western Serengeti and how does it influence attitude towards large predators and their conservation?

Paper I:

In Africa, only a handful of studies have attempted to quantify the cost inflicted on livestock keepers by predators, but up to now none have been conducted in Tanzania, despite being identified as one of the most important countries on the continent for large predator conservation. Livestock depredation in the villages in the western Serengeti is mostly caused by spotted hyena, followed by leopard, baboon (*Papio cynocephalus*), lion and jackal. The economic loss equals two-thirds of the annual cash income for the households in this area, and is a serious impediment to development. Depredation events are not only restricted to villages adjacent to the protected areas but affect households located relatively far away (>30 km). However, only spotted hyena is reported to cause loss in these households, whereas depredation by the large felids is concentrated along the protected area boundary. Tolerance of livestock loss is very low and the majority accept retaliatory killing as a way to reduce loss. Education, the number of livestock lost and the perceived effectiveness of protective measures influence acceptance of retaliatory killing, which suggests that conservation efforts should concentrate on identifying causes of losses, improving protective measures and providing better educational opportunities in the villages.

Bushmeat hunting in the western Serengeti and effects on wildlife (Paper II-IV)

Illegal bushmeat hunting has been identified as the main threat towards the ecological integrity of the Serengeti ecosystem. Here I describe the occurrence of bushmeat hunting and some of its effects on wildlife populations.

Paper II:

Prey choice of hunters, in relation to sex and age of animals killed, is of relevance to the sustainability of harvesting levels. Illegal hunters in the western Serengeti use a wide variety of hunting methods, where the majority of the offtake is composed of migratory species. Wire snares were mostly used for large herbivores, whereas for small and medium-sized prey hunting at night with dogs was common. Passive hunting methods (i.e. snares, staked pitfalls) had a tendency for a male bias in kills. Hunting methods where the hunter(s) actively stalked the prey resulted in more males being killed, as well as more immature animals than adults. The primitive hunting technology used indicates that the male-bias in kills is likely to be a result of behavioural factors among the prey species, rather than deliberate choice of the hunters.

Paper III:

Due to the secrecy of illegal hunting, a direct assessment of activities and pressure is often difficult and time consuming to conduct. The use of behaviour and demography has therefore been proposed as indicators of exploitation. Impala is the most common resident herbivore in the Serengeti, and is also a preferred species by illegal hunters. Densities of impala were found to be significantly lower outside the Serengeti National Park, as well as in sections of the National Park close to human settlements, than in the core. Furthermore, although there were no differences in group size outside and inside the protected area, the sex ratio was skewed towards females in the areas outside the National Park. Impala also took flight more easily and the flight initiation distance was greater outside than inside. Since both legal resident hunting and trophy hunting have small quotas on impala, illegal bushmeat hunting is probably the reason for the observed differences. This raises concern for the situation of other resident herbivores in the western Serengeti.

Paper IV:

The perceived risk is important when deciding when to flee from an approaching predator that appears threatening. This could be done by the prey either through monitoring the distance to

an approaching threat or by estimating the expected time it would take the predator to arrive at their location. Animals are expected to adjust their flight initiation distance, length of flight and speed according to a cost-benefit trade-off when facing predation risk. However, Thomson's gazelles did not vary flight initiation distance according to increased predation risk. However, fast approaches caused higher flight speeds, although it had no effect on flight length. In addition, we found that gazelles appeared to display their escape capabilities through condition dependent signals when the perceived threat was high. These results support that animals use distance as a cue to evaluate when to flee (i.e. spatial margin of safety), instead of estimating the expected time that the predator would take to reach them (i.e. temporal margin of safety). Moreover, alarm signals may convey important clues on the perceived level of predation risk.

Performance of community-based conservation (Paper V-VI)

Wildlife related benefits distributed to local communities rely on compensating for the costs of wildlife (i.e. crop and livestock damage, costs of not engaging in illegal hunting). Does the game cropping operation of SRCP offset the potential costs of refraining from illegal bushmeat hunting? In addition, law enforcement is widely regarded as essential in controlling unwanted human behaviour. However, very little information exists on local law enforcement units' ability to police wildlife resources on their village land.

Paper V:

Game cropping has been conducted by SRCP since 1993 in order to provide project villages with incentives to stop illegal bushmeat hunting. But the quotas allocated to each village are small, has a low level of participation by local people and is not economically sustainable without donor support. The cropping operation provides low levels of benefits to the individual villager, compared to the potential benefits generated through engaging in bushmeat hunting. Moreover, illegal hunting is mainly done for subsistence reasons, and illegal hunting is extensive around both project and other villages. SRCP should instead focus on other ways of diversifying income opportunities for the project villages.

Paper VI:

Local people are unlikely to comply with conservation objectives if benefit levels are not linked in some way to conservation friendly behaviour. Law enforcement is therefore widely accepted as a prerequisite in controlling illegal activities. Village game scouts employed by

the villages part of SRCP revealed, through patrols conducted in the partially and non-protected village lands, that illegal hunting activity varies temporally, and high activity coincides with the arrival of the wildebeest migration. All illegal hunters originated from local villages within a catchment zone of < 41 km from the closest protected area border. The probability of making arrests was influenced by season, the total number of illegal hunters observed when on patrol and the interaction between these two values. Support from district level units had only minor importance in the probability of making arrests. This indicates that when establishing the new protected area category called Wildlife Management Areas in Tanzania, one cannot expect Village Game Scouts to be able to reduce hunting if not supported by adequately funded district units.

Discussion

The results presented here show that local people bear substantial costs related to wildlife, and that CBC falls short of offsetting these costs. Illegal bushmeat hunting is very common outside the Serengeti National Park, but local law enforcement may provide a way to control and monitor illegal activities in some areas.

Costs of conservation

Humans living adjacent to protected areas or outside protected areas where natural habitats still sustain large mammal populations can bear substantial costs related to crop damage, livestock injury and loss or even human injury and death (Hoare 2000; Packer et al. 2005). Livestock loss occurs wherever large predator ranges and livestock distribution overlaps, and in rural Africa encroachment on protected areas is increasing the rate of the conflict. Previous studies have shown a wide regional variation in the frequency of carnivore attacks by different species (Kruuk 1980; Butler 2000; Patterson et al. 2004), where the observed variation has been explained by differences in relative densities of large predators (Kolowski and Holekamp 2006; Paper I), livestock husbandry practices (Kruuk 1980; Ogada et al. 2003; Paper I), or relative abundance of different livestock species (Rasmussen 1999; Butler 2000; Patterson et al. 2004). Similarly to the study of Kolowski and Holekamp (2006) located in the pastoral areas adjacent to Masai Mara National Reserve in Kenya (see Figure 3), spotted hyenas dominate the livestock loss in the western Serengeti. The prevalence of spotted hyena as the most numerous large predator in the Serengeti ecosystem probably contribute to this, together with the species' adaptability to anthropogenic environments. Moreover, in high density areas, human activity and persecution probably cause predators to become more active

during the night, thereby making the construction of night time enclosures crucial to restrict livestock loss, since during the day livestock is herded.

Livestock keepers usually have a low tolerance of livestock loss. Particularly among small scale subsistence farmers depredation can be catastrophic, and may have negative secondary effects on wildlife through retaliatory killing (Ogada et al. 2003) or through seeking alternative protein and income sources, such as bushmeat (Johannesen 2006). Consequently, protected area borders can for predator populations act as population sinks, which could potentially threaten their viability (Woodroffe and Ginsberg 1998; Loveridge et al. 2006). Understanding the reasons for negative attitudes towards carnivores is therefore a salient issue for reduction of the conflict level and for potentially decreasing the willingness to recuperate losses by killing predators. Studies show that livestock owners are more negative towards carnivores than others and that the general acceptability of carnivores is low when human life is threatened (Kleiven et al. 2004; Kaltenborn et al. 2006). In Europe and North America, especially older people, women and people who suffer an economic loss due to carnivores have a more negative attitude towards these species (Kellert 1985; Røskaft et al. 2003; Kleiven et al. 2004; Kaltenborn et al. 2006). Moreover, the loss of domestic dogs has also been implicated in negative attitudes towards carnivores (Kojola and Kuittinen 2002). In the western Serengeti, attitudes were negative irrespective of sex and age group. In accordance with previous studies, approval of retaliatory killing was positively related to sustained livestock loss. Furthermore, a contributing factor to negative attitudes might have been the general feeling of insecurity, since spotted hyenas may break into houses during the night to prey on domestic dogs. Studies also confirm that spotted hyenas are among the least liked large predators in Africa (Lindsey et al. 2005; Kaltenborn et al. 2006). Education is essential in this respect both to improve alternative income opportunities and challenge misconceptions (Rasmussen 1999; Loibooki et al. 2002). In addition, improving protection measures for livestock can to a certain extent be an alternative to lethal control, especially in the case of management of endangered carnivores. Improved protection measures might also lead to beneficial secondary effects in terms of reducing the level of illegal bushmeat hunting which is a serious problem in the Serengeti National Park, since it is mostly the poor households that have few livestock that engage in this activity (Loibooki et al. 2002). However, where livestock depredation has a serious impact despite preventive measures or where carnivores are a threat to human safety, lethal control may remain as the only management tool, since translocation of large carnivores has not been very successful (Linnell 1997). Alternatively, using trophy hunting to take care of problem individuals might be an

option (Lindsey et al. 2006). In Zimbabwe, this strategy has reduced the number of animals being killed (Child 2005). However, the existence of “problem individuals” is debated (Linnell et al. 1999).

Bushmeat hunting in the western Serengeti

Inside the Serengeti National Park, wire snaring is the main hunting method because of its relatively low probability of being detected by law enforcement personnel (Arcese et al. 1995). However, studies indicate that the methods used for hunting by local people are more diverse in the absence of control (i.e. staked pitfalls, use of nets, self-made traps, poisoned darts or arrows) (Arcese et al. 1995; FitzGibbon et al. 1995; Paper II, V). The main target prey appear to be migratory herbivores, which is in accordance with earlier studies (Arcese et al. 1995; Campbell and Hofer 1995; Hofer et al. 1996). Low-tech hunting techniques are generally assumed to be unselective with respect to sex and age (Arcese et al. 1995; Mduma et al. 1998). However, sex and age classes differ in their risk prone behaviour, which might influence their vulnerability to being killed by human hunters (FitzGibbon 1998). A sex-biased hunting has clear relevance for the sustainability of harvesting levels (Ginsberg and Milner-Gulland 1994; Mduma et al. 1998). Although the sample size is small, there is a tendency for males to be killed more often both by active (bows and arrows) and passive (i.e. snares, staked pitfalls) hunting methods. However, for some species, such as wildebeest, grouping patterns might by chance cause only males to be caught. Accordingly, sex ratio counts of the wildebeest population do not support a highly male biased hunting (Mduma et al. 1998).

Paper III found a female biased sex ratio for impala in areas outside the national park, which is in contrast to earlier studies in Africa (Caro 1999b). However, differences between areas might be influenced by prevalent hunting methods, as well as hunting pressure. It has been suggested in previous studies that male-biased hunting pressure may limit population size because female fecundity may be reduced when trophy males are removed (Fairall 1985; Ginsberg and Milner-Gulland 1994). However, most of the evidence indicates that extreme sex ratio biases (<5 males per 100 females) are required to affect population productivity, although adverse effects for some species have been shown (Ginsberg and Milner-Gulland 1994; Solberg et al. 2002). Illegal bushmeat hunting is also probably the main cause for reduced densities of impala in the partially protected areas and the areas inside the national park closest to human settlements.

Increased group size has been suggested to be an adaptive response to increasing predation risk (FitzGibbon 1998). However, paper (III) demonstrated that impala does not

respond to increased hunting pressure by increasing group size. But there are several other factors that may play a role in influencing group size. Mating system has been implicated, as well as the availability and concentration of forage resources for the animals, where rich food patches are associated with a larger group size than poor ones (Gude et al. 2006).

Hunting also affects wildlife behaviour, which might be of relevance for conservation if changes are costly in terms of reductions in food intake levels (Blumstein et al. 2005), increased stress hormone levels (Buchanan 2000) or leads to greater exposure to predation (Sinclair and Arcese 1995a; Kilgo et al. 1998). There are now several studies that report a change in anti-predator behaviour (as a result of hunting), such as wariness (e.g. white-tailed deer (*Odocoileus virginianus*) (Kilgo et al. 1998); roe deer (*Capreolus capreolus*) (de Boer et al. 2004); Paper III). In the Katavi ecosystem in western Tanzania, Caro (1999a) reported that species that were more likely to flee also occurred at lower densities outside the National Park boundary, suggesting that they were subject to hunting. Accordingly, in paper III it was showed that impalas became more wary and densities of impala were lower outside than inside the Serengeti National Park. It also appears that, at least for Thomson's gazelle, animals primarily use distance to the source of threat to assess risk, and that alarm signals may convey additional cues on the perception of threat (Paper IV).

In this context an important question for management is how representative are the changes observed for impala for other resident species in the Serengeti? Impala has a relatively high reproductive rate (Fairall 1983, 1985), compared to other resident herbivores, such as giraffe, buffalo and topi (see Campbell and Hofer 1995). It is also probably more tolerant to disturbance, since it is widely used in game ranching (Fairall 1985). Observed changes for impala might therefore underestimate the effect of bushmeat hunting for other more vulnerable species. For instance, topi populations in the Serengeti appear to be in a decline compared to other resident herbivores (Rusch et al. 2005). However, interspecific prey preferences of illegal hunters might also influence the generality of the results.

Performance of community-based conservation

Wildlife utilisation is a common way of extending benefits to the local communities' part of CBCs (Lewis et al. 1990; Macnab 1991; Sinclair and Arcese 1995b; Child 1996; Songorwa 1999; Walsh 2000). The abundant wildlife in many regions of East Africa has also earlier inspired proposals of centrally organised game cropping operations to utilise the vast herbivore herds (Myers 1981). However, findings on game cropping operations have concluded that ungulate cropping in East Africa is an uncertain endeavour, in terms of logistic

demands, access to adequate markets for products and disturbance of wildlife and tourism (Parker 1984; Macnab 1991). Only a handful of operations have been successful and they have not been in wilderness areas, but on well-developed land (Parker 1984). Likewise, the SRCP game cropping operation was not economically sustainable, and the level of participation was limited (Paper V). Other CBCs in Tanzania implemented more participatory community hunting schemes. For example, Village Game Scouts in the Selous Conservation Project are issued firearms and have the responsibility of hunting the wildlife quota for their village (Songorwa 1999). But the security situation in the early 1990s probably made such an approach impossible in the Serengeti, and traditional hunting techniques were evaluated to have low effectiveness and judged to be unethical (Hough 1993).

A few studies have been critical to the wildlife utilisation that is emphasised by CBCs (Macnab 1991; Barrett and Arcese 1995; Sinclair and Arcese 1995b). Partly, this has been due to that wildlife contains several biological and socio-economic constraints that may limit their value to conservation (Barrett and Arcese 1995). Wildlife has a limited growth rate and a steadily diminishing habitat at their disposal. Therefore connecting increasing human demands to harvesting might in the long term lead to demands of increasing the harvesting level to unsustainable limits (i.e. to maintain the per capita benefit), or difficulties at reducing offtake when productivity is low. Nevertheless, CBCs practice sustainable use and quotas are usually set very conservatively (Songorwa 1999; Walsh 2000; Paper V). For example, the SRCP game cropping operation had in 2001 an offtake of only 412 animals (Holmern et al. 2004). This offtake is clearly within sustainable limits for the migratory herbivores, which has been estimated for wildebeest to be approximately 56,000-74,000 animals with a dry season rainfall of 150mm (Pascual et al. 1996; Mduma et al. 1998). Similarly, trophy hunting, which also is used by CBC initiatives to generate income, typically removes only 2-5% of the male population (Creel and Creel 1997; Greene et al. 1998). Trophy hunting also generates high revenues per client and has a low environmental impact compared to photographic tourism. But hunting of carnivore species requires caution, since the removal of trophy sized males, for example in lions, can lead to infanticide, affect social stability and increase the vulnerability to kleptoparasitism (Cooper 1991; Yamazaki 1996; Whitman et al. 2004).

Illegal bushmeat hunting outside the Serengeti National Park is primarily done for subsistence reasons, and the people engaging in the activity are usually poor and have few or no livestock (Paper V; Loibooki et al. 2002). Commercial motives are also present where revenues are used to pay taxes and school fees for children. Increased integration in a cash based economy will undoubtedly place heavy strains on existing sources of income generation.

Refraining from illegal hunting could therefore be costly, if alternative protein and income sources are not provided. Likewise, continued illegal hunting has also been reported from other CBC areas, where there has also been pointed out that hunting has a cultural aspect that has not been currently addressed (Gibson and Marks 1995; Lewis and Phiri 1998; Kaltenborn et al. 2005).

Sharing of wildlife related benefits might not be the only way of improving relationships and creating incentives for conservation. Salafsky et al (2001) indicated that non-cash benefits such as education and development of trust among partners in a CBC project may be an alternative path to conservation success. A number of studies exploring conservation attitudes of local people indicate an improved relationship between local people and protected areas after the establishment of CBCs. For example, Kidegesho et al. (2006) found that villages participating in the SRCP in the western Serengeti had better perception of adjacent protected areas than non-project villages. Around the Selous Game Reserve people had better conservation attitudes when having access to wildlife related benefits than those that did not (Gillingham and Lee 1999). Interaction with protected area staff has also improved relationships (Newmark et al. 1993). However, there is an urgent need to establish in which extent attitudes are related to behaviour, but attitudinal surveys offer at least an initial assessment of changes in the perception of the value of conservation.

A key element for establishing control mechanisms for human behaviour is law enforcement. Species protection laws by themselves have no influence on prey choice of hunters (Rowcliffe et al. 2004). For instance, Caro et al. (1998) found that National Parks and Game Reserves in Tanzania had higher densities of large ungulates than Game Controlled Areas and Open Areas, and attributed this largely to the presence of on site law enforcement. Although law enforcement inside National Parks may contribute in reducing exploitation levels (Hilborn et al. 2006), in many cases detection rates are too low for effective exclusion of illegal resource extraction (Hofer et al. 2000; Abbot and Mace 1999). For example, in Malawi National Park, even in areas with the highest patrol efforts, the risk of detection appeared still to favour illegal wood collection (Abbott and Mace 1999). Yet, there is a consensus that increased detection rate is better at deterring illegal hunting than increased penalty level, especially in situations where opportunity costs are low (Leader-Williams and Milner-Gulland 1993). Compared to local bushmeat hunters, organised well-armed illegal trophy hunting groups respond less to detection rates and penalties (Milner – Gulland and Leader Williams 1992), and effective measures to curb illegal trophy hunting must therefore focus on delivering appropriate sentences to the organisers, which suggest that local law

enforcement has little to contribute in this respect. Collaboration between local law enforcement, such as the Village Game Scouts, and other more professional units is therefore important.

Management recommendations

Limited resources are a recurrent problem in conservation, therefore identifying the areas and issues in most need of attention is of primary importance (Sinclair and Arcese 1995b). For large predator conservation, finding ways of improving protection measures for livestock in the western Serengeti would be very beneficial, both in terms of reducing the incentives for retaliatory killings, but also for improving the relationship with adjacent protected areas. Such efforts should also be implemented in other parts of the Serengeti ecosystem where other endangered carnivores (e.g. African wild dogs) are struggling to survive.

CBC in the western Serengeti has tried to address a wide array of challenges over a huge area, but should instead concentrate on the areas that are most important for wildlife and have the conditions for becoming self-sustainable. Baseline data, such as wildlife population monitoring, is a prerequisite for any future evaluation of these efforts, but has in previous projects seldom been implemented with adequate expertise, if at all (Kremen et al. 1994). Including behavioural parameters in monitoring schemes could thus be an efficient way at giving an initial crude measure of which species that are experiencing heavy hunting pressure. Particularly, frequency of flight behaviour, can be a good indicator that is easy to implement and applicable with little training.

Several studies now underline the importance of connecting benefits and behaviour in CBCs (Mishra et al. 2003; Johannesen 2006). A possibility for CBCs is therefore to link wildlife related incentives to enforcement effort, as well as to other possible parameters of performance (i.e. wildlife densities). Nevertheless, the performance of Village Game Scouts will likely be site specific and related to the type and severity of hunting pressure. Forging a good co-operation between Village Game Scouts, District units, as well as TANAPA rangers is therefore vital. However, law enforcement in partially protected areas is generally grossly under-funded, and ways of alleviating this situation should be explored. A possibility is using revenue retention schemes that have been used with some success to boost law enforcement in the Selous Game Reserve (Balduş et al. 2003).

Future prospects

Reducing conflicts between wildlife and people is crucial for the long term maintenance of wildlife populations and the public support of protected areas (Newmark et al. 1993). Identifying the causes of livestock loss and the environmental factors linked to them, as well as the spatial and temporal distribution of depredation will be of importance for conflict resolution. Experimental approaches should also be tried out in order to reveal the effectiveness of protection measures. Linking questionnaire derived data to spatial distribution through geographic information systems (GIS), might also reveal more clearly where conservation efforts need to focus. However, methods to verify losses should be incorporated to improve the reliability of the data.

Using behavioural indicators can be a cost effective way of getting a crude measure of which species are most affected by illegal hunting. However, their effectiveness depends on hunting pressure and whether hunters have preferences for certain species or not. Investigating multiple species, might thus give a better indication of the extent of the hunting pressure, as well as reveal if there are interspecific differences. Although flight initiation distance is a commonly used metric, other variables such as alert distance and time to re-engaging in original behaviour might be better parameters at describing sensitivity to disturbance.

It is important that ways of verifying the efficiency of local law enforcement are implemented. Future studies should also explore more in detail how patrolling effort relates to illegal activities, by using longer time series. This might especially be important in a migratory system like the Serengeti, where the migration routes vary according to the prevalent rainfall pattern.

References

- Abbot, J.I.O., Mace, R., 1999. Managing protected woodlands: fuelwood collection and law enforcement in Lake Malawi National Park. *Conservation Biology* 13: 418-421.
- Adams W.M., Hulme D., 2001. If community conservation is the answer in Africa, what is the question? *Oryx* 35: 193-200.
- Alpert, P., 1996. Integrated conservation and development projects. *BioScience* 46: 845-855.
- Alvard, M.S., 1993. Testing the “Ecological Nobel Savage” Hypothesis: interspecific prey choice by Piro hunters of Amazonian Peru. *Human Ecology* 21: 355-387.
- Arcese, P., Hando, J., Campbell, K., 1995. Historical and present day anti-poaching efforts in Serengeti. In: Sinclair, A.R.E., Arcese, P., (Eds.), *Serengeti II - Dynamics, management, and conservation of an ecosystem*. The University of Chicago Press, pp. 506-533.
- Augustine, D.J., McNaughton, S.J., 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems* 9: 1242-1256.
- Baldus, R.D., Cauldwell, A.E., 2004. Tourist hunting and its role in development of wildlife management areas in Tanzania. *Sixth international Game Ranching Symposium, Paris*, 45 pp.
- Baldus, R., Kibonde, B., Siege, L., 2003. Seeking conservation partnerships in the Selous Game Reserve, Tanzania. *Parks* 13: 50-61.
- Balmford, A., Moore, J.L., Brooks, T., Burgess, N., Hansen, L.A., Williams, P., Rahbek, C., 2001. Conservation conflicts across Africa. *Science* 291: 2616-2619.
- Barnes, J.I., MacGregor, J., 2002. Economic efficiency and incentives for change within Namibia’s Community Wildlife Use Initiatives. *World Development* 30: 667-681.
- Barnes, R.F.W., Kapela, E.B., 1991. Changes in the Ruaha elephant population caused by poaching. *African Journal of Ecology* 29: 289-294.
- Barnett, R., 2000. Food for thought: The utilization of Wild Meat in Eastern and Southern Africa. Nairobi, Kenya: TRAFFIC East/Southern Africa, 264 pp.
- Barrett, C.B., Arcese, P., 1995. Are integrated conservation-development projects (ICDPS) sustainable? On the Conservation of large mammals in sub-Saharan Africa. *World Development* 23: 1073-1084.
- Berkes, F., 2004. Rethinking community-based conservation. *Conservation Biology* 18: 621-630.

- Bertram, B.C.R., 1979. Serengeti predators and their social systems. In: Sinclair, A.R.E., Norton-Griffiths, M., (Eds.), Serengeti - Dynamics of an ecosystem. The University of Chicago Press, pp. 221-248.
- Bertram, B.C.R., 1982. Leopard ecology as studied by radio tracking. Symposium of the Zoological Society of London 49: 341-352.
- Blaut, J.M., 1993. The colonizer's model of the world: Geographical diffusionism and Eurocentric history. New York, Guilford Press.
- Blumstein, D.T., 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour* 71: 389-399.
- Blumstein, D.T., Fernández-Juricic, E., Zollner, P.A., Garity, S.C., 2005. Interspecific variation in anti-predator behaviour and human-wildlife coexistence. *Journal of Applied Ecology* 42: 943-953.
- Bonner, R., 1993. At the Hand of Man- Peril and Hope for Africa's Wildlife. New York, Vintage Books.
- Boone, R.B., Thirgood, S.J., Hopcraft, G.C., 2006. Serengeti wildebeest migratory patterns modelled from rainfall and new vegetation growth. *Ecology* 87: 1987-1994.
- Borge, A., 2003. Essays on the economics of African wildlife and utilization and management. Dr.polit. thesis, Norwegian University of Science and Technology, Trondheim, Norway, 187 pp.
- Brashares, J.S., Arcese, P., Sam, M.K., Coppolillo, P.B., Sinclair, A.R.E., Balmford, A., 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science* 306: 1180-1183.
- Buchanan, K.L., 2000. Stress and the evolution of condition dependent signals. *Trends in Ecology and Evolution* 15: 156-160.
- Butler, J.R.A., 2000. The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. *African Journal of Ecology* 38: 23-30.
- Campbell, K.L.I., Borner, M., 1995. Population trends and distribution of Serengeti herbivores: Implications for management. In: Sinclair, A.R.E., Arcese, P., (Eds.), Serengeti II - Dynamics, management, and conservation of an ecosystem. The University of Chicago Press, pp. 117-145.
- Campbell, K.L.I., Hofer, H., 1995. People and wildlife: Spatial dynamics and zones of interaction. In: Sinclair, A.R.E., Arcese, P., (Eds.), Serengeti II - Dynamics, management, and conservation of an ecosystem. The University of Chicago Press, pp. 534-570.

- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309: 1239-1241.
- Caro, T.M., 1994. *Cheetahs of the Serengeti plains: Group living in an asocial species.* Chicago, University of Chicago Press.
- Caro, T.M., 1999a. Densities of mammals in partially protected areas: the Katavi ecosystem of western Tanzania. *Journal of Applied Ecology* 36: 205-217.
- Caro, T.M., 1999b. Demography and behaviour of African mammals subject to exploitation. *Biological Conservation* 91: 91-97.
- Caro, T.M., Durant, S.M., 1995. The importance of behavioural ecology for conservation biology: Examples from Serengeti carnivores. In: Sinclair, A.R.E., Arcese, P., (Eds.), *Serengeti II - Dynamics, management, and conservation of an ecosystem.* The University of Chicago Press, pp. 451-472
- Caro, T.M., Pelkey, N., Borner, M., Campbell, K.L.I., Woodworth, B.L., Farm, B.P., Ole Kuwai, J., Huish, S.A., Severre, E.L.M., 1998. Consequences of different forms of conservation for large mammals in Tanzania: preliminary analyses. *African Journal of Ecology* 36: 303-320.
- Chape S., Harrison J., Spalding M., Lysenko I., 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society B-Biological Sciences* 360: 443-455.
- Chapin, M., 2004. A challenge to conservationists. *World Watch* magazine (November/December). Worldwatch institute. pp.17-31.
- Child, B., 1996. The practice and principles of community based wildlife management in Zimbabwe: the CAMPFIRE programme. *Biodiversity and Conservation* 5: 369-398.
- Child, B., 2005. Principles, practice and results of CBNRM in southern Africa. <http://sandcounty.net/assests/chapters/assests.pdf>.
- Cincotta, R.P., Wisnewski, J., Engelman, R., 2000. Human population in the biodiversity hotspots. *Nature, London* 404: 990-992.
- Cole, D.N., Landres, P.B., 1996. Threats to wilderness ecosystems: Impacts and research needs. *Ecological Applications* 6: 168-184.
- Cooper, S.M., 1991. Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyenas. *African Journal of Ecology* 29: 130-136.
- Creel, S., Creel, N.M., 1997. Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. *African Journal of Ecology* 35: 83-93.

- de Boer, H.Y., van Breukelen, L., Hootsmans, M.J.M., van Wieren, S.E., 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. *Wildlife Biology* 10: 35-41.
- Dobson, A., 1995. The ecology and epidemiology of rinderpest virus in Serengeti and Ngorongoro Conservation Area. In: Sinclair, A.R.E., Arcese, P., (Eds.), *Serengeti II - Dynamics, management, and conservation of an ecosystem*. The University of Chicago Press, pp. 485-505.
- Drews, C., 1995. Road kills of animals by public traffic in Mikumi National Park, Tanzania, with notes on baboon mortality. *African Journal of Ecology* 33: 89-100.
- Dublin, H.T., Douglas-Hamilton, I., 1987. Status and trends of elephants in the Serengeti-Mara ecosystem. *African Journal of Ecology* 25: 19-33.
- Dublin, H.T., Sinclair, A.R.E., Boutin, S., Anderson, E., Jago, M., Arcese, P., 1990. Does competition regulate ungulate populations? Further evidence from Serengeti, Tanzania. *Oecologia* 82: 283-288.
- du Toit, J.T., 2002. Wildlife harvesting guidelines for community-based wildlife management: A southern African perspective. *Biodiversity and Conservation* 11: 1403-1416.
- du Toit, J.T., Cumming, D.H.M., 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation* 8: 1643-1661.
- Edroma, E.L., Kenyi, J.M., 1985. Drastic decline in bohor reedbuck (*Redunca redunca* Pallas 1977) in Queen Elizabeth National Park, Uganda. *African Journal of Ecology* 23: 53-55.
- Estes, R.D., 1990. *The Safari Companion: A guide to watching African mammals*. Chelsea Green Publishing Company, Post Mills, Vermont, USA.
- Fairall, N., 1983. Production parameters of the impala *Aepyceros melampus*. *South African Journal of Animal Science* 13: 176-179.
- Fairall, N., 1985. Manipulation of age and sex-ratios to optimize production from impala *Aepyceros melampus* populations. *South African Journal of Wildlife Research* 15: 85-88.
- FitzGibbon, C.D., 1998. The management of subsistence harvesting: Behavioural ecology of hunters and their mammalian prey. In: Caro, T., (Ed.), *Behavioral ecology and conservation biology*. Oxford University Press. pp. 449-473.
- FitzGibbon, C.D., Mogaka, H., Fanshawe, J.H., 1995. Subsistence hunting in Arabuko-Sokoke Forest, Kenya and its effects on mammal populations. *Conservation Biology* 9: 1116-1126.

- Frame, L.H., Malcolm, J.R., Frame, G.W., van Lawick, H., 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti plains, Tanzania 1967-1978. *Zeitschrift für Tierpsychologie* 50: 225-249.
- Fryxell, J.M., Greever, J., Sinclair, A.R.E., 1988. Why are migratory ungulates so abundant? *American Naturalist* 131: 781-98.
- Foxcroft, L.C., Lotter, W.D., Runyoro, V.A., Mattay P.M.C., 2006. A review of the importance of invasive alien plants in the Ngorongoro Conservation Area and Serengeti National Park. *African Journal of Ecology* 44: 404–406.
- Gereta, E., 2004. Transboundary water issues threaten the Serengeti ecosystem. *Oryx* 38: 13-16.
- Gibson, C.C., Marks, S.A., 1995. Transforming rural hunters into conservationists - An assessment of community-based wildlife management programs in Africa. *World Development* 23: 941-957.
- Ginsberg, J.R., Milner-Gulland, E.J., 1994. Sex-biased harvesting and population dynamics in ungulates: Implications for conservation and sustainable use. *Conservation Biology* 8: 157-166.
- Greene, C., Umbanhowar, J., Mangel, M., Caro, T., 1998. Animal breeding systems, hunter selectivity, and consumptive use in wildlife conservation. In: Caro, T. (Ed.), *Behavioural Ecology and Conservation Biology*. Oxford University Press, New York. pp. 271-305.
- Gros, P.M., 2002. The status and conservation of cheetah *Acinonyx jubatus* in Tanzania. *Biological Conservation* 106: 177-185.
- Gude, J.A., Garrott, R.A., Borkowski, J.J., King, F., 2006. Prey risk allocation in a grazing ecosystem. *Ecological Applications* 16: 285-298.
- Hackel, J.D., 1999. Community Conservation and the Future of Africa's Wildlife. *Conservation Biology* 13: 726-734.
- Haltenorth, T., Diller, H., 1996. *Mammals of Africa including Madagascar*. Harper Collins.
- Handby, J.P., Bygott, J.D., 1979. Population changes in lions and other predators. In: Sinclair, A.R.E., Norton-Griffiths, M., (Eds.), *Serengeti - Dynamics of an ecosystem*. The University of Chicago Press. pp. 249-262.
- Hilborn, R., Arcese, P., Borner, B., Hando, J., Hopcraft, G., Loibooki, M., Mduma, S., Sinclair, A.R.E., 2006. Effective enforcement in a conservation area. *Science* 314: 1266. doi: 10.1126/science.1132780
- Hoare, R., 2000. African elephants and humans in conflict: The outlook for co-existence. *Oryx* 34: 34-38.

- Hofer, H., Campbell, K.L.I., East, M.L., Huish, S.A., 1996. The impact of game meat hunting on target and non-target species in the Serengeti. In: Taylor, J., Dunstone, N., (Eds.), The exploitation of mammal populations. Chapman and Hall, London, pp. 117-146.
- Hofer, H., Campbell, K.L.I., East, M.L., Huish, S.A., 2000. Modelling the spatial distribution of the economic costs and benefits of illegal game meat hunting in Serengeti. *Natural Resource Modelling* 13: 151-177.
- Hofer, H., East, M.L., 1995. The commuting system of Serengeti spotted hyenas: how a predator copes with migratory prey. I. Social organization. *Animal Behaviour* 46: 547-557.
- Hofer, H., East, M.L., Campbell, K.L.I., 1993. Snares, commuting hyenas and migratory herbivores: humans as predators in the Serengeti. *Symposium of the Zoological Society of London* 65: 347-366.
- Holmern, T., Johannesen, A.B., Mbaruka, J., Mkama, S., Muya, J., Røskaft, E., 2004. Human-wildlife conflicts and hunting in the western Serengeti, Tanzania. NINA Report 26. Norwegian Institute for Nature Research, Trondheim, Norway.
- Homewood, K., Lambin, E.F., Coast, E., Kariuki, A., Kikula, I., Kivelia, J., Said, M., Serneels, S., Thompson, M., 2001. Long-term changes in Serengeti-Mara wildebeest and land cover: Pastoralism, population, or policies? *Proceedings of the National Academy of Science U.S.A.* 98: 12544-12549.
- Hough, J.L., 1993. Community Hunting Experiments. Technical Report No.2. Serengeti Regional Conservation Strategy.
- Höner, O.P., Wachter, B., East, M.L., Runyoro, V.A., Hofer, H., 2005. The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. *Oikos* 108: 544-554.
- Jachmann, H., Billiouw, M., 1997. Elephant poaching and law enforcement in the central Luangwa Valley, Zambia. *Journal of Applied Ecology* 34: 233-244.
- Jarman, P.J., 1974. The social organisation of antelope in relation to their ecology. *Behaviour* 48: 215-267.
- Johannesen, A.B., 2006. Designing integrated conservation and development projects (ICDPs): Illegal hunting, wildlife conservation, and the welfare of the local people. *Environment and Development Economics* 11: 247-267.
- Kaltenborn, B.P., Bjerke, T., Nyahongo, J.W., Williams, D.R., 2006. Animal preferences and acceptability of wildlife management actions around Serengeti National Park, Tanzania. *Biodiversity and Conservation* 15: 4633-4649.

- Kaltenborn, B.P., Nyahongo, J.W., Tingstad, M.K., 2005. The nature of hunting around the Western Corridor of Serengeti National Park, Tanzania. *European Journal of Wildlife Research* 51: 213-222.
- Kellert, S.R., 1985. Public perceptions of predators, particularly the wolf and coyote. *Biological Conservation* 31: 167-189.
- Kidegesho, J.R., Røskaft, E., Kaltenborn, B.P., (online) Factors influencing conservation attitudes of local people in Western Serengeti, Tanzania. *Biodiversity and Conservation*. doi: 10.1007/s10531-006-9132-8
- Kilgo, J.C., Labisky, R.F., Fritzen, D.E., 1998. Influences of hunting on the behaviour of white-tailed deer: implications for conservation of the Florida panther. *Conservation Biology* 12: 1359-1364.
- Kiss A., (Ed.). 1990. Living with wildlife: Wildlife resource management with local participation in Africa. World Bank Technical Paper Number 130, Washington, D.C., USA.
- Kleiven, J., Bjerke, T., Kaltenborn, B.P., 2004. Factors influencing the social acceptability of large carnivore behaviours. *Biodiversity and Conservation* 13: 1647-1658.
- Kolowski, J.M., Holekamp, K.E., 2006. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation* 128: 529-541.
- Kojola, I., Kuittinen, J., 2002. Wolf attacks on dogs in Finland. *Wildlife Society Bulletin* 30: 498-501.
- Kremen, C., Merenlender, A.M., Murphy, D.D., 1994. Ecological monitoring: A vital need for integrated conservation and development programs in the tropics. *Conservation Biology* 8: 388-397.
- Kruuk, H., 1972. The spotted hyena: a study of predation and social behaviour. The University of Chicago Press. Chicago.
- Kruuk, H., 1980. The effect of large carnivores on livestock and animal husbandry in Marsabit District, Kenya. IPAL Technical Report E – 4 (ITE Project 675), 52 pp.
- Leader-Williams, N., Albon, S.D., 1988. Allocation of resources for conservation. *Nature*, London 336: 533-535.
- Leader-Williams, N., Albon, S.D., Berry, P.S.M., 1990. Illegal exploitation of black rhinoceros and elephant populations: patterns of decline, law enforcement and patrol effort in Luangwa Valley, Zambia. *Journal of Applied Ecology* 27: 1055-1087.

- Levine, A., 2002. Convergence or convenience? International conservation NGOs and development assistance in Tanzania. *World Development* 30: 1043-1055.
- Lewis, D.M., Alpert, P., 1997. Trophy hunting and wildlife conservation in Zambia. *Conservation Biology* 11: 59-68.
- Lewis, D.M., Kaweche, G.B., Mwenya, A., 1990. Wildlife conservation outside protected areas- lessons from an experiment in Zambia. *Conservation Biology* 4: 171-180.
- Lewis, D.M., Phiri, A., 1998. Wildlife snaring - an indicator of community response to a community-based conservation project. *Oryx* 32: 111-121.
- Lindsey, P.A., du Toit, J.T., Mills, M.G.L., 2005. Attitudes of ranchers towards African wild dogs *Lycaon pictus*: Conservation implications on private land. *Biological Conservation* 125: 113-121.
- Lindsey, P.A., Roulet, P.A., Romañach, S.S., 2006. Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation*. doi: 10.1016/j.biocon.2006.09.005.
- Linnell, J.D.C., Aanes, R., Swenson, J.E., Odden, J., Smith, M.E., 1997. Translocation of carnivores as a method for managing problem animals: a review. *Biodiversity and Conservation* 6: 1245-1257.
- Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R., Swenson, J.E., 1999. Large carnivores that kill livestock: do "problem individuals" really exist? *Wildlife Society Bulletin* 27:698-705.
- Loibooki, M., Hofer, H., Campbell, K.L.I., East, M.L., 2002. Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. *Environmental Conservation* 29: 391-398.
- Loveridge, A.J., Searle, A.W., Murindagomo, F., Macdonald, D.W., 2006. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*. doi: 10.1016/j.biocon.2006.09.010.
- Lyons, K.G., Brigham, C.A., Traut, B.H., Schwartz, M.W., 2005. Rare species and ecosystem functioning. *Conservation Biology* 19: 1019-1024.
- Mabunda, D., Pienaar, D.J., Verhoef, J., 2003. The Kruger National Park: A century of management and research. In: du Toit, J.T. Rogers, K.H. Biggs. H.C. (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington D.C., pp.3-21.
- Macnab, J., 1991. Does game cropping serve conservation? A re-examination of the African data. *Canadian Journal of Zoology* 69: 2203-2290.

- Maddock, L., 1979. The "migration" and grazing succession. In: Sinclair, A.R.E., Norton-Griffiths, M., (Eds.), Serengeti - Dynamics of an ecosystem. The University of Chicago Press, pp. 104-129.
- Madhusudan, M.D., 2004. Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology* 41: 858-869.
- Mbano B.N.N., Malpas, R.C., Maige, M.K.S., Symonds, P.A.K., Thompson, D.M., 1995. The Serengeti Regional Conservation Strategy. In: Sinclair, A.R.E., Arcese, P., (Eds.), Serengeti II - Dynamics, management, and conservation of an ecosystem. The University of Chicago Press, pp. 605-616.
- McClanahan, T., Davies, J., Maina, J., 2005. Factors influencing resource users and managers' perceptions towards marine protected area management in Kenya. *Environmental Conservation* 32: 42-49.
- Mduma, S.A.R., Hilborn, R., Sinclair, A.R.E., 1998. Limits to exploitation of Serengeti wildebeest and implications for its management. In: Newbery, D.M., Underwood, H.B., Prins, H.H.T., (Eds.), Dynamics of tropical communities. Blackwell Science, Oxford, pp. 243-265.
- Mills, G., Hofer, H., 1998. Hyenas: status survey and conservation action plan. World Conservation Union, Gland, Switzerland.
- Milner-Gulland, E.J., Leader-Williams, N., 1992. A model of incentives for the illegal exploitation of black rhinos and elephants: Poaching pays in Luangwa Valley, Zambia. *Journal of Applied Ecology* 29: 388-401.
- Mishra, C., Allen, P., McCarthy, T., Madhusudan, M.D., Bayarjargal, A., Prins, H.H.T., 2003. The role of incentive programs in conserving the snow leopard. *Conservation Biology* 17: 1512-1520.
- Mulongoy, K.J., Chape, S., 2004. Protected areas and biodiversity: An overview of key issues. CBD Secretariat, Montreal, Canada and UNEP-WCMC, Cambridge UK. Available from: <http://www.unep-wcmc.org/resources/publications/UNEP_WCMC_bio_series/21.htm> (accessed 15 January 2007).
- Murray, M.G., 1982. Home range, dispersal and the clan system of impala. *African Journal of Ecology* 71: 907-915.
- Myers, N., 1981. The Canning of Africa. *Science Digest* 8: 72-119.
- Naiman, R.J., 1988. Animal influences on ecosystem dynamics. *BioScience* 38: 750-752.

- Naughton-Treves, L., Holland, M.B., Brandon, K., 2005. The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annual Review of Environment and Resources* 30: 219-252.
- Neumann, R.P., 1998. *Imposing wilderness: struggles over livelihood and nature preservation in Africa*. Berkley: University of California Press.
- Neumann, R.P., 2002. The postwar conservation boom in British colonial Africa. *Environmental History* 7: 22-47.
- Newmark, W.D., 1996. Insularization of Tanzanian parks and the local extinction of large mammals. *Conservation Biology* 10: 1549-1556.
- Newmark, W.D., Hough, J.L., 2000. Conserving wildlife in Africa: integrated conservation and development projects and beyond. *BioScience* 50: 585-592.
- Newmark, W.D., Leonard, N.L., Sariko, H.I., Gamassa, D.M., 1993. Conservation attitudes of local people living adjacent to five protected areas in Tanzania. *Biological Conservation* 63: 177-183.
- Nielsen, M.R., 2006. Importance, cause and effect of bushmeat hunting in the Udzungwa Mountains, Tanzania: Implications for community based wildlife management. *Biological Conservation*. 128: 509-516.
- Norton-Griffiths, M., 1996. Property rights and the marginal wildebeest: An economic analysis of wildlife conservation options in Kenya. *Biodiversity and Conservation* 5: 1557-1577.
- Ogada, M.O., Woodroffe, R., Oguge, N.O., Frank, L.G., 2003. Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology* 17: 1521-1530.
- Ottichilo, W.K., Leeuw, J., Prins, H.H.T., 2000. Population trends of resident wildebeest [*Connochaetes taurinus hecki* (Neumann)] and factors influencing them in Masai Mara ecosystem, Kenya. *Biological Conservation* 97: 271-282.
- Packer, C., 1990. Serengeti lion survey. Report to TANAPA, SWRI, MWEKA and the Game Department. Tanzania National Parks, Arusha, Tanzania.
- Packer, C., Altizer, S., Appell, M., Brown, E., Martenson, J., O'Brien, S.J., Roelke-Parker, M., Hofmann-Lehmann, R., Lutz, H., 1999. Viruses of the Serengeti: Patterns of infection and mortality in African lions. *Journal of Animal Ecology* 68: 1161-1178.
- Packer, C., Ikanda, D., Kissui, B., Kushnir, H., 2005. Lion attacks on humans in Tanzania. *Nature*, London 436: 927-928.

- Parker, I.S.C., 1984. Perspectives on wildlife cropping or culling. In: Bell, R.H.V., McShane-Caluzi, E., (Eds.), Conservation and wildlife resources in Africa. Washington, D.C. Peace Corps, pp. 233-253.
- Pascual, M.A., Kareiva, P., Hilborn, R., 1996. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. Conservation Biology 11: 966-976.
- Patterson, B.D., Kasiki, S.M., Selempo, E., Kays, R.W., 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighbouring Tsavo National Parks, Kenya. Biological Conservation 119: 507-516.
- Pelkey, N.W., Stoner, C.J., Caro, T.M., 2000. Vegetation in Tanzania: assessing long term trends and effects of protection using satellite imagery. Biological Conservation 94: 297-309.
- Phillips, A., 1999. Working landscapes as protected areas. In: Stolton, S., Dudley, N., (Eds.), Partnerships for protection/New strategies for planning and management for protected areas. London, UK: WWF International & IUCN, Earthscan Publications, pp. 205-214.
- Rasmussen, G.S.A., 1999. Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: a case study. Biological Conservation 88: 133-139.
- Ripple, W.J., Beschta, R.L., 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? Bioscience 54: 755-766.
- Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, C.M., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffman, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X., 2004. Effectiveness of the global protected area network in representing species diversity. Nature, London 428: 640-643.
- Rowcliffe, J.M., de Merode, E., Cowlshaw, G., 2004. Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. Proceedings of the Royal Society London B 271: 2631-2636.
- Røskoft E., Bjerke T., Kaltenborn B., Linnell J.D.C., Andersen R., 2003. Patterns of self-reported fear towards large carnivores among the Norwegian public. Evolution and Human Behaviour 24: 184-198.
- Rusch, G., Stokke, S., Røskoft, E., Mwakalebe, G., Wiik, H., Arnemo, J., Lyamuya, R., 2005. Human-wildlife interactions in western Serengeti, Tanzania. Effects of land management on migratory routes and mammal population densities. NINA Report 85, Trondheim, Norway, 47 pp.

- Salafsky, N., Cauley, H., Balachander, G., Cordes, B., Parks, J., Margolius, C., Bhatt, S., Encarnacion, C., Russell, D., Margolius, R., 2001. A systematic test of an enterprise strategy for community-based biodiversity conservation. *Conservation Biology* 15: 1585-1595.
- Schaller, G.B., 1972. *The Serengeti lion. A study of predator-prey relations*. Chicago University Press.
- Sinclair, A.R.E., Arcese, P., 1995a. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology* 76: 882-891.
- Sinclair, A.R.E., Arcese, P., 1995b. Serengeti in the context of worldwide conservation efforts. In: Sinclair, A.R.E., Arcese, P., (Eds.), *Serengeti II - Dynamics, management, and conservation of an ecosystem*. The University of Chicago Press, pp. 31-46.
- Sinclair A.R.E., Mduma S., Brashares J.S., 2003. Patterns of predation in a diverse predator-prey system. *Nature*, London 425: 288-290.
- Skarpe, C., Aarrestad, P.A., Andreassen, H.P., Dhillion, S.S., Dimakatso, T., du Toit, J.T., Halley, D.J., Hytteborn, H., Makhabu, S., Mari, M., Marokane, W., Masunga, G., Modise, D., Moe, S.R., Mojaphoko, R., Mosugelo, D., Motsumi, S., Neo-Mahupeleng, G., Ramotadima, M., Rutina, L., Sechele, L., Sejoe, T.B., Stokke, S., Swenson, J.E., Taolo, C., Vandewalle, M., Wegge, P., 2004. The return of the giants: Ecological effects of an increasing elephant population. *Ambio* 33: 276-282.
- Solberg, E., Loison, A., Ringsby, T.H., Sæther, B.E., Heim, M., 2002. Biased sex ratio can affect fecundity in primiparous moose *Alces alces*. *Wildlife Biology* 8: 117-128.
- Songorwa, A.N., 1999. Community-based wildlife management (CWM) in Tanzania: Are the communities interested? *World Development* 27: 2061-2079.
- Spinage, C., 1998. Social change and conservation misrepresentation in Africa. *Oryx* 32: 265-276.
- SRCP (Serengeti Regional Conservation Project) 1999. Annual Report July 1998 to June 1999. Ministry of Natural Resources and Tourism (Wildlife Department). Serengeti Regional Conservation Project.
- Stiles D., 2004. The ivory trade and elephant conservation. *Environmental Conservation* 31: 309-321.
- Terborgh, J., 1999. *Requiem for Nature*. Island Press. Washington D.C.
- Thirgood, S.J., Mosser, A., Tham, S., Hopcraft, J.G.C., Mwangomo, E., Mlengeya, T., Kilewo, M., Fryxell, J.M., Sinclair, A.R.E., Borner, M., 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation* 7: 113 – 120.

- Tobler, M.W., Cochard, R., Edwards, P.J., 2003. The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. *Journal of Applied Ecology* 40: 430–444.
- UN (United Nations) 2005. World population prospects: The 2004 revision. Population Division, United Nations, New York, USA, pp. 105. Available from: <<http://esa.un.org/unpp/>> (accessed 15 January 2007).
- UNEP-WCMC 2005. World database on protected areas. Available from: <<http://sea.unep-wcmc.org/wdbpa/>> (accessed 15 January 2007).
- URT (United Republic of Tanzania) 2002. 2002 Population and housing census. Available from: <<http://www.tanzania.go.tz/census/index.html>> (accessed 15 January 2007).
- URT (The United Republic of Tanzania) 2004. Reference manual for implementing guidelines for the designation and management of wildlife management (WMAs) in Tanzania. Ministry of Natural Resources and Tourism, Wildlife Division, Dar es Salaam. Government Printer.
- Voeten, M.M., Prins, H.H.T., 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* 120: 287-294.
- Walsh, M.T., 2000. The development of community wildlife management in Tanzania. Paper presented to the conference on: African wildlife management in the new millennium. 13-15 December 2000, College of African Wildlife Management, Mweka, Tanzania.
- Wells, M., Brandon, K., 1993. The principles and practice of buffer zones and local participation in biodiversity conservation. *Ambio* 22: 157-162.
- Wilkie, D.S., Carpenter, J.F., 1999. Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. *Biodiversity and Conservation* 8: 927 – 955.
- Whitman, K., Starfield, A.M., Quaddling, H.S., Packer, C., 2004. Sustainable trophy hunting of African lions. *Nature, London* 428: 175-178.
- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126-2128.
- WRI (World Resource Institute) 2005. Earth trends data tables: Biodiversity and protected areas. Washington D.C., World Resource Institute. Available from: <http://earthtrends.wri.org/country_profiles/index.php?theme=7> (accessed 2 March 2007).
- Yamazaki, K., 1996. Social variation of lions in a male-depopulated area in Zambia. *Journal of Wildlife Management* 60: 490-497.

Paper I

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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.

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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 main-

taining 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, Ogotu 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 predation 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 km²), 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 km²) 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 km²), Grumeti Game Reserve (ca. 416 km²) and the Ikoma Open Area (ca. 600 km²). 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/km²), 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

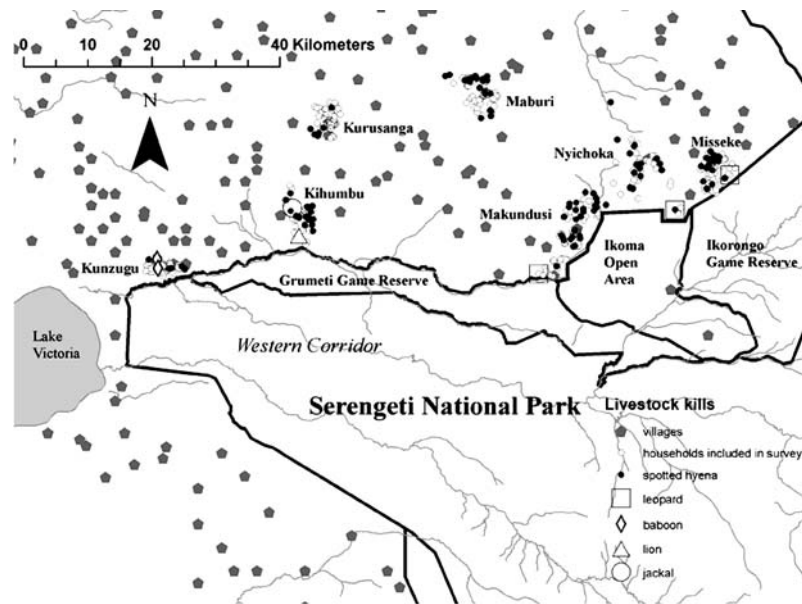


Fig. 1 – Distribution of reported livestock kills according to the predator responsible for the kill. The location of villages is shown as grey pentagrams, and the households from the seven villages included in the survey as open circles.

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 \times PA distance, education \times gender, education \times 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 (\pm 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 \pm 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 \pm 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% ($\pm 13.5\%$) of their livestock (considering all respondents) or 6.8% ($\pm 15.9\%$) 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% ($\pm 21.6\%$), 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 numerous 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 \times education	4	473.3	0.81	0.050
Education + PA distance + livestock owner + gender + age + PA distance \times education + gender \times education + age \times 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 \times education + gender \times education + age \times 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.

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

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
<i>Full data set (n = 411)</i>				
(Intercept)	−0.83	0.13	−6.46	<0.001
Education	−0.68	0.26	−2.56	0.011
<i>Only livestock keepers (n = 274)</i>				
(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	%
<i>Negative responses (agree)</i>	
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
<i>Positive responses (disagree)</i>	
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

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 Røskoft, 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 Skonhøft, 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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REFERENCES

- Baldus, R.D., Cauldwell, A.E., 2004. Tourist hunting and its role in development of wildlife management areas in Tanzania. In: Sixth international Game Ranching Symposium, Paris, 45pp.
- Borge, A., 2003. Essays on the economics of African wildlife and utilization and management. Dr.polit. thesis, Norwegian University of Science and Technology, Trondheim, Norway, 187pp.
- Boydston, E.E., Kapheim, K.M., Watts, H.E., Szykman, M., Holekamp, K.E., 2003. Altered behaviour in spotted hyena associated with increased human activity. *Animal Conservation* 6, 207–219.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer, Berlin.
- Butler, J.R.A., 2000. The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. *African Journal of Ecology* 38, 23–30.
- Campbell, K.L.I., Hofer, H., 1995. People and wildlife: spatial dynamics and zones of interaction. In: Sinclair, A.R.E., Arcese, P. (Eds.), *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem*. The University of Chicago Press, Chicago, pp. 534–570.
- Cardillo, M., Purvis, A., Secrest, W., Gittleman, J.L., Bielby, J., Mace, G.M., 2004. Human population density and extinction risk in the world's carnivores. *PLOS Biology* 2, 0909–0914.
- Fanshawe, J.H., Ginsberg, J.R., Sillero-Zubiri, C., Woodroffe, R., 1997. The status and distribution of remaining wild dog populations. In: Woodroffe, R., Ginsberg, J.R., Macdonald, D.W. (Eds.), *The African Wild Dog: Status Survey and Conservation Action Plan*, pp. 11–57.
- Frank, L.G., Woodroffe, R., Ogada, M.O., 2005. People and predators in Laikipia District, Kenya. In: Woodroffe, R., Thirgood, S., Rabinowitz, A. (Eds.), *People and Wildlife: Conflict or Coexistence?* Cambridge University Press, Cambridge, pp. 286–304.
- Graham, K., Beckerman, A.P., Thirgood, S., 2005. Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122, 159–171.
- Herfindal, I., Linnell, J.D.C., Moa, P.F., Odden, J., Austmo, L.B., Andersen, R., 2005. Does recreational hunting of lynx reduce depredation losses of domestic sheep? *Journal of Wildlife Management* 69, 1034–1042.
- Hofer, H., East, M.L., 1993. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. I. Social organization. *Animal Behaviour* 46, 547–557.
- Hofer, H., East, M.L., Campbell, K.L.I., 1993. Snares, commuting hyaenas and migratory herbivores: humans as predators in the Serengeti. *Symposia of the Zoological Society London* 65, 347–366.
- Hofer, H., Campbell, K.L.I., East, M.L., Huish, S.A., 1996. The impact of game meat hunting on target and non-target species in the Serengeti. In: Taylor, J., Dunstone, N. (Eds.), *The Exploitation of Mammal Populations*. Chapman and Hall, London, pp. 117–146.
- Holmern, T., Borge Johannesen, A., Mbaruka, J., Mkama, S., Muya, J., Røskaft, E., 2004. Human-wildlife conflicts and hunting in the western Serengeti, Tanzania. Norwegian Institute for Nature Research, Project Report 26, Trondheim, Norway, 26pp.
- IUCN The World Conservation Union, 2006. IUCN Red List of threatened species: A Global Assessment. Gland, Switzerland.
- Johannesen, A.B., 2006. Designing integrated conservation and development projects (ICDPs): illegal hunting, wildlife conservation, and the welfare of the local people. *Environment and Development Economics* 11, 247–267.
- Johannesen, A.B., Skonhøft, A., 2005. Tourism, poaching and wildlife conservation: what can integrated conservation and development projects accomplish? *Resource and Energy Economics* 27, 208–226.
- Kaltenborn, B.P., Bjerke, T., Nyahongo, J.W., Williams, D.R., 2006. Animal preferences and acceptability of wildlife management actions around Serengeti National Park, Tanzania. *Biodiversity and Conservation*, doi: 10.1007/s10531-005-6196-9.
- Karani, I.W., Dublin, H.T., Koehler, G.M., 1995. Livestock depredation by predators in pastoral areas adjacent to Masai Mara National Reserve, Kenya. In: Bisonette, J.A., Krausman, P.R. (Eds.), *Integrating People and Wildlife for a Sustainable Future*. Wildlife Society, Maryland, pp. 360–363.
- Kellert, S.R., 1985. Public perceptions of predators, particularly the wolf and coyote. *Biological Conservation* 31, 167–189.
- Kleiven, J., Bjerke, T., Kaltenborn, B., 2004. Factors influencing the social acceptability of large carnivore behaviours. *Biodiversity and Conservation* 13, 1647–1658.
- Kolowski, J.M., Holekamp, K.E., 2006. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation* 128, 529–541.
- Kruuk, H., 1972. *The Spotted Hyena: A Study of Predation and Social Behaviour*. The University of Chicago Press, Chicago.
- Kruuk, H., 1980. The effect of large carnivores on livestock and animal husbandry in Marsabit District, Kenya. IPAL Technical Report E – 4 (ITE Project 675), 52pp.

- Lindsey, P.A., du Toit, J.T., Mills, M.G.L., 2005. Attitudes of ranchers towards African wild dogs *Lycaon pictus*: conservation implications on private land. *Biological Conservation* 125, 113–121.
- Linnell, J.D.C., Smith, M.E., Odden, J., Kaczensky, P., Swenson, J.E., 1996. Strategies for the reduction of carnivore–livestock conflicts: a review. Norwegian Institute for Nature Research, Oppdragsmelding 443, Trondheim, Norway, 118pp.
- Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R., Swenson, J.E., 1999. Large carnivores that kill livestock: do “problem individuals” really exist? *Wildlife Society Bulletin* 27, 698–705.
- Linnell, J.D.C., Swenson, J., Andersen, R., 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* 4, 345–350.
- Løe, J., Røskaft, E., 2004. Large carnivores and human safety: a review. *Ambio* 33, 283–288.
- Loibooki, M., Hofer, H., Campbell, K.L.I., East, M., 2002. Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. *Environmental Conservation* 29, 298–391.
- Meriggi, A., Lovari, S., 1996. A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock. *Journal of Applied Ecology* 33, 1561–1571.
- Mills, G., Hofer, H., 1998. Hyenas: Status Survey and Conservation Action Plan. World Conservation Union, Gland, Switzerland.
- Mishra, C., 1997. Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation* 24, 338–343.
- Mishra, C., Allen, P., McCarthy, T., Madhusudan, M.D., Bayarjargal, A., Prins, H.H.T., 2003. The role of incentive programs in conserving the snow leopard. *Conservation Biology* 17, 1512–1520.
- Mizutani, F., 1993. Home range of leopards and their impact on livestock on Kenyan ranches. In: Dunstone, N., Gorman, M.L. (Eds.), *In Mammals as Predators*. Clarendon Press, Oxford, pp. 425–439.
- Newmark, W.D., 1996. Insularization of Tanzanian parks and the local extinction of large mammals. *Conservation Biology* 10, 1549–1556.
- Newmark, W.D., Hough, J.L., 2000. Conserving wildlife in Africa: integrated conservation and development projects and beyond. *BioScience* 50, 585–592.
- Nowell, K., Jackson, P., 1996. Status, Survey and Conservation Action Plan, Wild Cats. World Conservation Union, Gland, Switzerland.
- Ogada, M.O., Woodroffe, R., Ouge, N.O., Frank, L.G., 2003. Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology* 17, 1521–1530.
- Ogutu, J.O., Bhola, N., Reid, R., 2005. The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. *Animal Conservation* 265, 281–293.
- Packer, C., Altizer, S., Appell, M., Brown, E., Martenson, J., O’Brien, S.J., Roelke-Parker, M., Hofman-Lehman, R., Lutz, H., 2000. Viruses of the Serengeti: patterns of infection and mortality in African lions. *Journal of Animal Ecology* 68, 1161–1178.
- Packer, C., Ikanda, D., Kissui, B., Kushnir, H., 2005. Lion attacks on humans in Tanzania. *Nature* 436, 927–928.
- Patterson, B.D., Kasiki, S.M., Selempo, E., Kays, R.W., 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation* 119, 507–516.
- Rasmussen, G.S.A., 1999. Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: a case study. *Biological Conservation* 88, 133–139.
- R Development Core Team, 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rudnai, J., 1979. Ecology of lions in Nairobi National Park and the adjoining Kitengela Conservation Unit in Kenya. *African Journal of Ecology* 17, 85–95.
- Rusch, G., Stokke, S., Røskaft, E., Mwakalebe, G., Wiik, H., Arnemo, J., Lyamuya, R., 2005. Human–wildlife interactions in western Serengeti, Tanzania. Effects of land management on migratory routes and mammal population densities. NINA Report 85, 47pp.
- Sinclair, A.R.E., 1995. Serengeti past and present. In: Sinclair, A.R.E., Arcese, P. (Eds.), *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem*. The University of Chicago Press, Chicago, pp. 3–30.
- SPSS, 2005. SPSS for Windows. Release 14.0. SPSS Inc., Chicago, IL.
- Stahl, L.P., Vandel, J.M., Herrenschmidt, V., Migot, P., 2001. The effect of removing lynx in reducing attacks of sheep in the French Jura mountains. *Biological Conservation* 101, 15–22.
- Treves, A., Karanth, K.U., 2003. Human–carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17, 1491–1499.
- Treves, A., Naughton-Treves, L., Harper, E.K., Mladenoff, D.J., Rose, R.A., Sickley, T.A., Wydeven, A.P., 2004. Predicting human–carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology* 18, 114–125.
- URT United Republic of Tanzania, 2002. 2002 Population and housing census. <http://www.tanzania.go.tz/census/index.html> (accessed 15.06.2006).
- Wang, S.W., Macdonald, D.W., 2006. Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biological Conservation* 129, 558–565.
- Woodroffe, R., Frank, L.G., 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Animal Conservation* 8, 91–98.
- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280, 2126–2128.
- Woodroffe, R., Lindsay, P., Romanach, S., Stein, A., Ole Ranah, S.M.K., 2005. Livestock predation by endangered African wild dogs (*Lycaon pictus*) in northern Kenya. *Biological Conservation* 124, 225–234.
- World Bank, 2006. World Development Indicators database: Tanzania data profile. <http://devdata.worldbank.org/external/CPPProfile.asp?PTYPE=CP&CCODE=TZA> (accessed 15.06.2006).

Paper II

Intraspecific prey choice of bushmeat hunters outside the Serengeti National Park, Tanzania: a preliminary analysis

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In this study we investigated intraspecific prey choice of illegal bushmeat hunters outside the Serengeti National Park, Tanzania. During the study 151 animals belonging to 12 species were reported killed. The majority, 76%, of prey species were migratory herbivores. Night hunting with dogs was the most common hunting method for medium-sized prey (biomass ≤ 40 kg), while the majority of the large herbivores were killed by snares. When actively stalking, hunters killed more males of most of the species recorded, as well as more immatures than adults. Passive hunting also generally had a male-bias. This suggests that the male-bias in kills probably is more a result of behavioural factors among the animals, combined with poor hunting technology, than deliberate choice of the hunters.

Key words: bushmeat, hunting, conservation, Serengeti, sex ratio, Tanzania.

INTRODUCTION

Many community-based conservation (CBC) projects in southern Africa emphasize wildlife harvesting as an income generating activity (Western 1994). The involvement of local people in this activity varies from active participants to passive beneficiaries. CBCs follow an assumption that local people will take care of their wildlife resources when given management responsibility (Du Toit 2002). However, several studies show that co-management and increased community benefits do not necessarily curtail human exploitative behaviour, partly because benefits often are incremental at the individual level (Gibson & Marks 1995; Newmark & Hough 2000; Holmern *et al.* 2002). The detrimental effects of human exploitative behaviour have been seen in the past when hunter-gatherer societies caused the extinction of many large herbivores and birds in Africa (Owen-Smith 1988). It is therefore important to understand individual hunting behaviour, and how this influences the prey choice and sustainability.

In Tanzania, illegal bushmeat hunting in the Serengeti National Park (hereafter SNP) is an issue of concern. Hunters mainly originate from communities on the western side of the SNP (Campbell & Hofer 1995; Loibooki *et al.* 2002). The main hunting method inside the SNP is wire snaring.

Arcese *et al.* (1995) reported that the reason for actual harvests and interspecific prey preference of hunters was abundance and ease of capture. In this study we therefore focused on intraspecific (i.e. according to sex and age) prey choice of hunters outside the SNP. We predicted that, under the assumption that handling costs are equal across age and sex categories within species; hunters would take more males when actively stalking prey since they are larger and therefore more profitable. We furthermore predicted that hunters would select more adults than their proportion in the population. Passive hunting (snares and pitfalls) on the other hand was predicted to kill randomly i.e. according to sex and age ratios found in the wild.

METHODS

Study area

The study area (01°15'–3°30'S, 34°–36°E) was located adjacent to the western corridor of the SNP. The western corridor is buffered by Grumeti Game Reserve (c. 416 km²), while the Ikoma Open Area (c. 600 km²) and Ikorongo Game Reserve (c. 563 km²) lie to the northwest (Fig. 1) (for details see Sinclair 1995). During the dry season blue wildebeest (*Connochaetes taurinus*) migrate through these areas (Thirgood *et al.* 2004). The partially protected areas also contain some resident wild-

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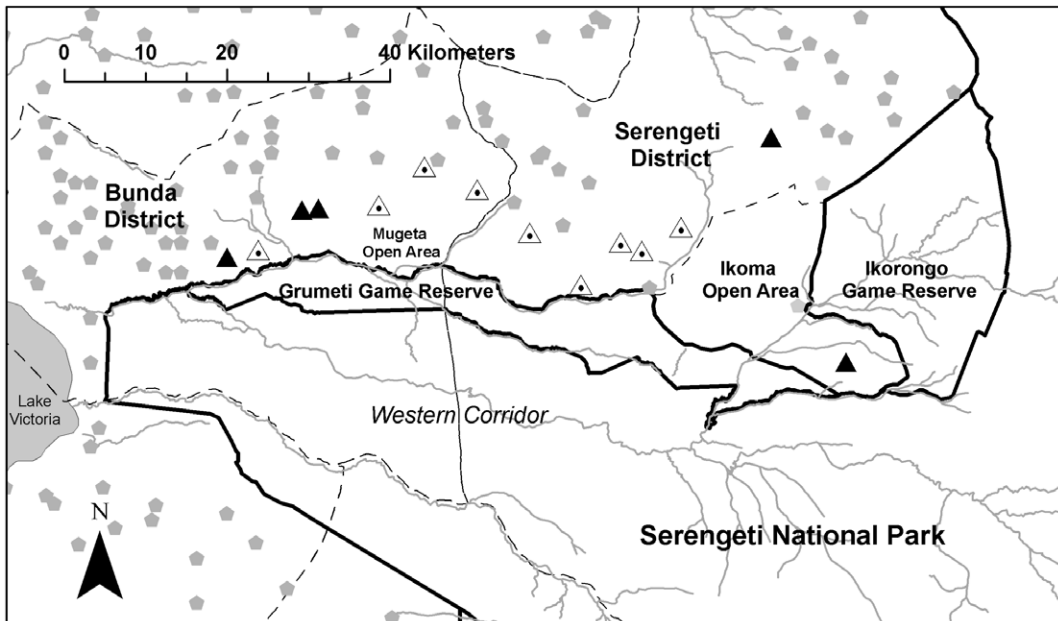


Fig.1. Map of the western corridor of the Serengeti National Park with the approximate locations of villages. Triangles are villages included in a CBC project and filled triangles are the five project villages included in the Village Game Scout survey. The grey pentagams are all other villages. The heavy dashed line represents district boundaries, thick lines denote the protected areas and the thin dashed line represents Ikoma Open Area.

life, although these are heavily reduced because of illegal bushmeat hunting from adjacent communities (Campbell & Borner 1995). Household consumption is the most important reason given for illegal hunting in the area outside the SNP (Holmern *et al.* 2002).

Data collection

Data on hunting were mainly collected through a questionnaire conducted during patrols by Village Game Scouts (VGS) in five selected communities from December 1998 to September 1999. In Bunda District, the VGS patrolled partly inside the adjacent Game Reserve, while in Serengeti District patrols were only done inside the Ikoma Open Area. The questionnaire contained information about: i) the patrol, ii) arrested hunter(s), and iii) method of hunting iv) species killed and sex and age class (adult, subadult and calf). We also placed special emphasis during discussions with the VGS to make sure we agreed upon the age classification, since we did not collect skulls in order to objectively assess the sex and age of killed animals. The species reported killed were either discovered snared by the VGS or they were based on replies from arrested hunters. We gave extensive explanations in how to use the question-

naires in close collaboration with the VGS, through follow-up meetings two times per month for the first three months and the last three months. These meetings also allowed for accountability. To test biases in sex ratio and age classes we used chi-square goodness of fit test with Yates correction (Zar 1998).

RESULTS

Prey choice and hunting methods

Hunters used an assortment of weapons to kill animals: spears, clubs, bow and arrows, snares and hunting dogs, but no firearms were reported (Table 1). The migratory species represented the bulk of the animals recorded (76.2%), as well as the percentage of usable meat (79.8%) (Table 1). The most important species in terms of percentage usable bushmeat was wildebeest (52.8% usable bushmeat), whereas the most commonly recorded species, Thomson's gazelle (*Gazella thomsoni*), constituted only 8.5%.

We classified the hunting methods into two groups: first, active hunting where the hunters stalked and killed the animal, and second, passive hunting (snares, spring traps and pit falls). Active hunting underlay 61.0% of the hunting mortality

Table 1. Hunting methods used by hunters to kill wildlife and percentage (in bold) of usable meat provided by each hunting method (M = migratory, R = resident).

Species groups	Animals (n)	Biomass (kg)	% Usable meat	Offtake in meat (kg)	Active hunting			Passive hunting			Pitfall	?
					Dog, torch & weapon*	Dog & weapon*	Weapon*	Snare	Spring trap	Pitfall		
Large herbivores					2.8	6.5	14.6	45.7	2.5	2.3	2.3	2.3
<i>Comochates taurinus</i> (M)	47	123	60 ^c	3468.6	1	5	13	24	1	2	2	2
<i>Equus burchelli</i> (M)	9	200	55 ^d	990	1			7				
<i>Damilliscus korrigum</i> (R)	5	100	60 ^e	300		1		4				
<i>Taurotragus oryx</i> (M)	1	340	65 ^c	221				1				
<i>Kobus ellipsipygmnus</i> (R)	1	160	55 ^c	88					1			
Medium/small herbivores					13.1	0.7	0.5	1.6	2.7	0.4	0.2	0.2
<i>Gazella thomsoni</i> (M)	58	15	64 ^c	556.8	51	5		3	2			
<i>Aepyceros melampus</i> (R)	18	40	65 ^d	468	12			1	2	1		
<i>Redunca redunca</i> (R)	4	40	65 ^e	104				1	3			
<i>Phacochoerus aethiopicus</i> (R)	3	45	65 ^c	87.8	1		1		1			
<i>Gazella granti</i> (M)	1	40	64 ^c	25.6	1							
<i>Sylvicapra grimmia</i> (R)	1	15	55 ^e	7.5								1
Other species								2.5	1.3			
<i>Struthio camelus</i> (R)	3	150	55 ^e	247.5				2	1			
Total	151			6564.8								

^aCoe et al. (1976), ^bGrzimek (1972), ^cBlumenschine & Caro (1986), ^dMarks (1973), ^econservative estimate based on lowest estimate; *topi assumed to be the same as wildebeest and reedbeek the same as impala; *weapon = club, machete, spear, bow and arrow.

(Table 1). Night hunting with flashlights, weapons and hunting dogs was the overall most common method of hunting (44.4%). For the medium-sized prey (biomass ≤ 40 kg), Thomson's gazelle and impala (*Aepyceros melampus*), 88% and 66.7%, respectively, were killed during night hunting. The passive methods represented 37.1% of the hunting mortality. Passive hunting methods were most common for the large animals (72.9% of hunting mortality). Wildebeest was the major species in passive hunting (44.1%). For the larger prey species (biomass > 40 kg) wire snares accounted for 85.7% of the animals killed.

Sex and age distribution

When actively stalking, hunters took a significantly higher proportion of male Thomson's gazelles (Table 2; $\chi^2 = 14.2$, d.f. = 1, $P < 0.01$). On the other hand the results indicate that hunters killed wildebeest according to prey availability ($\chi^2 = 1.1$, d.f. = 1, N.S.). There were more immatures killed than expected by active hunting for Thomson's gazelle (Table 2; $\chi^2 = 106.2$, d.f. = 1, $P < 0.01$). In regards to passive hunting more wildebeest males were killed ($\chi^2 = 12.7$, d.f. = 1, $P < 0.01$), while for the other species there was a slight numerical tendency for a higher representation of males (Table 3).

DISCUSSION

The results presented here suggest that a variety of hunting methods is used in the Serengeti. Outside the SNP, where law enforcement is virtually absent, hunters actively stalk their prey. The risk of injury by large prey probably confines stalking, such as night hunting, to the medium-sized and smaller prey species. In our study area, no hunters carrying firearms were reported, but hunters using firearms might have escaped capture since VGS

Table 2. Sex ratio and prey mortality by age of animals killed by active hunting methods (immature = subadult and calf).

Species	Sex ratio			Prey mortality by age		
	Males	Females	Sex ratio in population (m:f)	Adult	Immature	Age distribution in the population (ad:imm)
1. <i>Gazella thomsoni</i>	28	25	1:2.5 ^{a**}	13	40	1:0.23 ^{b**}
2. <i>Connochates taurinus</i> ^c	4	15	1:1.86 ^{NS}	4	15	–
3. <i>Aepyceros melampus</i>	5	2	–	7	–	–
4. <i>Damiliscus korrigum</i>	1	–	–	–	1	–
5. <i>Phacochoerus aethiopicus</i>	1	1	–	–	1	–
6. <i>Sylvicapra grimmia</i>	1	–	–	–	1	–

^aFitzGibbon (1990); ^bBradley (1977); ^cSex ratio of adults from Mduma (1996).

** $P < 0.01$.

only carry traditional weaponry on patrols, and the results might therefore not reflect the whole range of hunting methods. However, data from inside the SNP, where rangers are armed, confirm that firearms are very unusual. In other parts of Africa hunting with firearms is more common, although the use of snares and traps appears to be the most prevalent method (Marks 1973; Arcese *et al.* 1995; FitzGibbon *et al.* 1995; Goldspink *et al.* 1998; Noss 1998). In addition, some tribes in Southern and Central Africa practice traditional bow and net hunting (Wilkie *et al.* 1998; Hawkes *et al.* 2001).

In this study, migratory wildlife constituted the majority of prey taken by hunters and snaring of large herbivores contributed nearly half of the harvest in terms of meat. The same trend was also observed inside SNP where migratory prey constituted the majority of the harvest, although resident wildlife made up a larger percentage than the

harvest on the outside (Arcese *et al.* 1995; Holmern *et al.* 2002).

Few studies report the sex ratio of prey harvests from bushmeat hunters, but the handful that provide data show a male bias (Table 4). In our study, hunters killed significantly more male Thomson's gazelles when actively hunting, mainly by night hunting. Even non-human predators tend to have a male bias in their kills, and it has been suggested that this can be attributed to behavioural differences between the sexes (Prins & Iason 1989; FitzGibbon & Lazarus 1995; FitzGibbon 1998). For instance, the African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*) and hyaena (*Crocuta crocuta*) kill more adult males of Thomson's gazelles (Kruuk 1972; Fanshawe & FitzGibbon 1989; FitzGibbon 1990). Females are generally more vigilant and flee more frequently from predators than males (FitzGibbon 1998). In Thomson's gazelle, males are less vigilant,

Table 3. Sex ratio and prey mortality by age of animals killed by passive hunting methods (immature = subadult and calf).

Species	Sex ratio			Prey mortality by age		
	Males	Females	Sex ratio in population (m:f)	Adult	Immature	Age distribution in the population
<i>Gazella thomsoni</i>	–	2	–	2	–	–
<i>Connochates taurinus</i>	14	4	1:1.86 ^{a**}	7	8	–
<i>Aepyceros melampus</i>	4	–	–	3	1	–
<i>Equus burchelli</i>	6	1	–	5	2	–
<i>Damiliscus korrigum</i>	2	–	–	2	1	–
<i>Redunca redunca</i>	2	–	–	1	2	–
<i>Struthio camelus</i>	1	1	–	2	–	–
<i>Phacochoerus aethiopicus</i>	1	–	–	–	1	–
<i>Kobus ellipsiprymnus</i>	1	–	–	–	1	–

^aSex ratio of adults from Mduma (1996).

** $P < 0.01$.

Table 4. Studies of bushmeat hunting in Africa reporting sex biases in mammals across different locations, species and hunting methods.

Reference	Description of habitat & location	Species	Main hunting method	Sex bias
Marks 1973	Mixed savanna and mopane forest, Luangwa Valley, Zambia	Buffalo (<i>Syncerus caffer</i>) Impala (<i>Aepyceros melampus</i>)	Shotgun	Male bias
Edroma & Kenyi 1985	Tall grass shoreline, Queen Elizabeth National Park, Uganda	Bohor reedbuck (<i>Redunca redunca</i>)	?	Male bias
Georgiadis 1988 (<i>in</i> Campbell & Hofer 1995)	Open and wooded savanna, Serengeti National Park, Tanzania	Wildebeest (<i>Connochaetes taurinus</i>)	Snares	Male bias
Hofer <i>et al.</i> 1993	Open and wooded savanna, Serengeti National Park, Tanzania	Wildebeest	Snares	Male bias
Goldspink <i>et al.</i> 1998	Floodplains, Kasanka National Park, Zambia	Puku (<i>Kobus vardoni</i>)	Snares	Male bias
Mduma <i>et al.</i> 1998	Open and wooded savanna, Serengeti National Park, Tanzania	Wildebeest	Snares	None
Fischer & Linsenmair 2002	Open and wooded savanna, Comoe National Park, Ivory Coast	Kob (<i>Kobus kob kob</i>)	Shotgun, snares	Male bias

concentrate on the edges of groups, have greater nearest-neighbour distances and have lower flight distances to approaching predators (Walther 1979; Fanshawe & FitzGibbon 1989; FitzGibbon 1990).

Bushmeat hunters, however, killed wildebeest according to availability when actively hunting, probably because wildebeest migrate partly in mixed groups during the dry season and the lack of large sexual dimorphism makes differential hunting pressure difficult (Talbot & Talbot 1963). Moreover, the poor hunting technology probably further precludes prey choice.

For impala, Setsaas (2004) reported a sex ratio of one male to 2.1 females in the populations outside the SNP, which is significantly lower than inside the SNP (1:1.6). Illegal bushmeat hunting in the areas outside the SNP is severe, and it may therefore indicate that hunting not only has reduced population levels, but also altered the sex ratio. A skew in sex ratio as a result of high illegal hunting pressure on males has also recently been suggested by Fischer & Linsenmair (2002) for West African kob (*Kobus kob kob*). Bushmeat hunting in Africa might therefore be a contributing factor to the female bias observed in many wildlife populations.

For Thomson's gazelle we found that hunters killed more immatures than adults. A numerical tendency for this was also apparent for wildebeest. A preference for immatures, relative to availability, has also been found in carnivores (FitzGibbon & Lazarus 1995). By contrast, Marks (1973) reported that in Zambia the Valley Bisa hunters who hunt with firearms concentrated on adult animals. Similar results are reported by Fischer & Linsenmair (2002) for West African kob. Alvard (1995) found that Piro hunters in the Amazon, who hunt with shotguns, had an adult bias in the two most important prey items, collard peccary (*Tayassu tajacu*) and red brocket deer (*Mazama americana*), whereas the rest were indistinguishable from the censused populations. It has been suggested that immature animals might be easier to kill due to their risk prone behaviour and inexperience, thus increasing the exposure to predators and hunters compared to adults (FitzGibbon 1998). The hunting methods in the Serengeti may therefore limit the range of choice of animals available to the hunter.

For passive hunting methods, there seems to be a general tendency for males to be more easily caught, although we must emphasize that the sample sizes are low. Males have generally a more risk-prone behaviour than females and are more

active during mating and territorial behaviour (FitzGibbon 1998). For instance, both Georgiadis (1988: *in* Campbell & Hofer 1995) and Hofer *et al.* (1993) reported that the majority of wildebeest caught in snares were males. The reason for this was attributed to greater willingness of male groups to enter thickets and to the tendency for males to be at the front of herds as they move into new areas. However, Mduma *et al.* (1998) reported that data on sex ratio counts of the wildebeest population do not support a large male-biased harvesting, and suggested that the tendency of wildebeest to segregate into same-sex groups might by chance give a catch of one sex in small samples.

Prey choice has been explored by using optimal foraging theory (Alvard 1993, 1995). In Amazonian Peru the Piro hunters selected prey according to optimal foraging theory and did not withhold from harvesting species identified as vulnerable to over-hunting and local extinction. Intraspecific prey choice also indicated that they did not selectively choose individuals that minimize the impact on prey populations. Our results indicate that hunters in the Serengeti have few opportunities for a sex or age class choice, probably due to their current hunting methods. These data do not, therefore, provide strong support for the optimal foraging hypothesis. We suggest that the male and immature age bias observed in our data may rather be explained as a consequence of behavioural factors among the hunted animals that make certain sex or age groups more prone to be killed.

From a human conservation point of view, a male-biased hunting may be beneficial for a polygynous species, such as wildebeest, and increase the sustainable harvest. Nevertheless, there is increasing evidence that highly male-biased harvesting can have serious long-term negative implications for wildlife populations (Ginsberg & Milner-Gulland 1994; Mysterud *et al.* 2002). The harvesting of immatures may be advantageous for sustainability, since immatures contribute little to recruitment.

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REFERENCES

- ALVARD, M. 1993. Testing the 'Ecologically Noble Savage' Hypothesis: interspecific prey choice by Piro hunters of Amazonian Peru. *Human Ecology* **21**: 355–387.
- ALVARD, M. 1995. Intraspecific prey choice by Amazonian hunters. *Current Anthropology* **36**: 789–818.
- ARCESE, P., HANDO, J. & CAMPBELL, K.L.I. 1995. Historical and present day anti-poaching efforts in Serengeti. In: *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem*, (eds) A.R.E. Sinclair & P. Arcese, pp. 506–532. University of Chicago Press, Chicago.
- BLUMENSCHINE, R.J. & CARO, T.M. 1986. Unit flesh weights of some East African bovids. *African Journal of Ecology* **24**: 273–286.
- BRADLEY, R.M. 1977. Aspects of the ecology of Thomson's gazelle in the Serengeti National Park, Tanzania. Ph.D. thesis, Texas A & M University, Texas.
- CAMPBELL, K.L.I. & BORNER, M. 1995. Population trends and distribution of Serengeti herbivores: implications for management. In: *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem*, (eds) A.R.E. Sinclair & P. Arcese, pp. 117–145. University of Chicago Press, Chicago.
- CAMPBELL, K.L.I. & HOFER, H. 1995. People and wildlife: spatial dynamics and zones of interaction. In: *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem*, (eds) A.R.E. Sinclair & P. Arcese, pp. 534–570. University of Chicago Press, Chicago.
- COE, M.J., CUMMING, D.H., & PHILLIPSON, J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* **22**: 341–54.
- DU TOIT, J.T. 2002. Sustainable wildlife utilisation in Africa: a contest between scientific understanding and human nature. In: *Psychology of Sustainable Development*, (eds) P. Schmuck & W.P. Schultz, pp. 197–207. Kluwer Academic, Boston.
- EDROMA, E.L. & KENYI, J.M. 1985. Drastic decline in bohor reedbuck (*Redunca redunca* Pallas 1977) in Queen Elizabeth National Park, Uganda. *African Journal of Ecology* **23**: 53–55.
- FANSHAWE, J.H. & FITZGIBBON, C. 1989. Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour* **45**: 479–490.
- FISCHER, F. & LINSENMAIR, K.E. 2002. Demography of a West African kob (*Kobus kob kob*) population. *African Journal of Ecology* **40**: 130–137.
- FITZGIBBON, C. 1990. Why do hunting cheetahs prefer male gazelles? *Animal Behaviour* **40**: 837–845.
- FITZGIBBON, C. 1998. The management of subsistence harvesting: behavioural ecology of hunters and their mammalian prey. In: *Behavioral Ecology and Conservation Biology*, (ed.) T. Caro, pp. 449–473. Oxford University Press, Oxford.
- FITZGIBBON, C. & LAZARUS, J. 1995. Antipredator Behaviour of Serengeti Ungulates: Individual differ-

- ences and population consequences. In: *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem*, (eds) A.R.E. Sinclair & P. Arcese, pp. 274–296. University of Chicago Press, Chicago.
- FITZGIBBON, C., MOGAKA, H. & FANSHAW, J.H. 1995. Subsistence hunting in Arabuko-Sokoke Forest, Kenya, and its effects on mammal populations. *Conservation Biology* **9**: 1116–1126.
- GEORGIADIS, N. 1988 (in CAMPBELL & HOFER 1995). People and wildlife: spatial dynamics and zones of interaction. In: *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem*, (eds) A.R.E. Sinclair & P. Arcese, pp. 534–570. University of Chicago Press, Chicago.
- GIBSON, C.C. & MARKS, S.A. 1995. Transforming rural hunters into conservationists – an assessment of community-based wildlife management programs in Africa. *World Development* **23**: 941–957.
- GINSBERG, J.R. & MILNER-GULLAND, E.J. 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. *Conservation Biology* **8**: 157–166.
- GOLDSPINK, C.R., HOLLAND, R.K., SWEET, G. & STJERNSTEDT, R. 1998. A note on the distribution and abundance of puku, *Kobus vardoni* Livingstone, in Kasanka National Park, Zambia. *African Journal of Ecology* **36**: 23–33.
- GRZIMEK, B. 1972. *Grzimek's Animal Life Encyclopedia*. Birds I. Vol. 7. Van Nostrand Reinhold, New York.
- HAWKES, K., O'CONNEL, J.F., BLURTON JONES, N.G. 2001. Hadza meat sharing. *Evolution and Human Behaviour* **22**: 113–142.
- HOFER, H., EAST, M.L. & CAMPBELL, K.L.I. 1993. Snares, commuting hyaenas and migratory herbivores: humans as predators in the Serengeti. *Symposia of the Zoological Society, London* **65**: 347–366.
- HOLMERN, T., RÖSKAFT, E., MBARUKA, J., MKAMA, S.Y. & MUYA, J. 2002. Uneconomical game cropping in a community-based conservation project outside the Serengeti National Park, Tanzania. *Oryx* **36**: 364–372.
- KRUUK, H. 1972. *The Spotted Hyena: a Study of Predation and Social Behaviour*. University of Chicago Press, Chicago.
- LOIBOOKI, M., HOFER, H., CAMPBELL, K.L.I. & EAST, M. 2002. Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. *Environmental Conservation* **29**: 391–298.
- MARKS, S.A. 1973. Prey selection and annual harvest of game in a rural Zambian community. *East African Journal of Ecology* **11**: 113–128.
- MDUMA, S.A.R. 1996. Serengeti wildebeest population dynamics: regulation, limitation and implications for harvesting. Ph.D. thesis, University of British Columbia, Vancouver.
- MDUMA, S.A.R., HILBORN, R., SINCLAIR, A.R.E. 1998. Limits to exploitation of serengeti wildebeest and implications for its management. In: *Dynamics of Tropical Communities*, (eds) D.M. Newberry, H.H.T. Prins & N.D. Brown, pp. 243–265. Blackwell Science, Oxford.
- MYSTERUD, A., COULSON, T. & STENSETH, N.C. 2002. The role of males in the dynamics of ungulate populations. *Journal of Animal Ecology* **71**: 907–915.
- NEWMARK, W.D. & HOUGH, J.L. 2000. Conserving wildlife in Africa: integrated conservation and development projects and beyond. *Bioscience* **50**: 585–592.
- NOSS, A.J. 1998. The impacts of cable snare hunting on wildlife populations in the forest of the Central African Republic. *Conservation Biology* **12**: 390–398.
- OWEN-SMITH, R.N. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge.
- PRINS, H.H.T. & IASON, G.R. 1989. Dangerous lions and nonchalant buffalo. *Behaviour* **108**: 262–296.
- SETSAAS, T.H. 2004. How does human exploitation affect impala (*Aepyceros melampus*) populations in protected and partially protected areas? – a case study from the Serengeti ecosystem, Tanzania. M.Sc. thesis, Norwegian University of Science and Technology, Trondheim.
- SINCLAIR, A.R.E. 1995. Serengeti past and present. In: *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem*, (eds) A.R.E. Sinclair & P. Arcese, pp. 3–30. University of Chicago Press, Chicago.
- TALBOT, L.M. & TALBOT, M.H. 1963. The wildebeest in western Masailand, East Africa. *Wildlife Monographs* **12**.
- THIRGOOD, S.J., MOSSER, A., THAM, S., HOPCRAFT, J.G.C., MWANGOMO, E., MLENGEYA, T., KILEWO, M., FRYXELL, J.M., SINCLAIR, A.R.E. & BORNER, M. 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation* **7**: 113–120.
- WALTHER, F. 1969. Flight and avoidance of predators in Thomson's gazelles (*Gazella thomsoni* Gunther 1884). *Animal Behaviour* **25**: 713–719.
- WESTERN, D., WRIGHT, M. & STRUM, S.C. 1994. *Natural Connections: Perspectives in Community-based Conservation*. Island Press, Washington, D.C.
- WILKIE, D.S., CURRAN, B., TSHOMBE, R. & MORELLI, G.A. 1998. Managing bushmeat hunting in Okapi Wildlife Reserve, Democratic Republic of Congo. *Oryx* **32**: 131–144.
- ZAR, J.H. 1998. *Biostatistical Analysis*, 4th edn. Prentice-Hall International Inc., Upper Saddle River, NJ.

Paper III

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How does human exploitation affect impala populations in protected and partially protected areas? – A case study from the Serengeti Ecosystem, Tanzania

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Tanzania

ABSTRACT

Human exploitation can have severe conservation implications for wildlife populations. In the Serengeti ecosystem, Tanzania, illegal hunting is a serious concern for wildlife management, and in this study we investigated if density, demography and behaviour can be used as indicators of human exploitation. We used impala (*Aepycerus melampus*) as a model species to study human exploitation inside and outside a strictly protected area. Over a six month period, a total of 2050 km of transects were driven in the different protected areas (National Park, Game Reserve, Open Area). Densities were estimated by using distance sampling and the partially protected areas were found to have significantly lower densities (4.3 ind/km²) than the National Park (15.3 ind/km²). A variation in density between different sections within the National Park was also found. However, we found no differences in group sizes. Moreover, the sex-ratio was more skewed towards females in the partially protected areas and in sections within the National Park close to villages. In addition, impalas showed higher alertness levels, and longer flight initiation distance to an approaching human in the partially protected areas compared to the National Park. The present harvest levels by illegal hunting in the study area are most likely the cause of the observed differences. Our results suggest that density, demography and behaviour can be used as indicators of human exploitation, but that this probably varies according to local hunting pressure. Furthermore, it could be expected that the results obtained in this study might reflect the state of other ungulates in the area, which raises concern whether management objectives for the buffer zones of Serengeti National Park are met.

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1. Introduction

There is considerable concern over the steadily increasing human impact and encroachment on remaining unprotected

natural habitats, as well as protected area networks, in developing countries. Studies examining ecological impacts across gradients of human disturbance are therefore fundamental in understanding the effect of human populations on natural

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ecosystems (Caro, 1999a). Partially protected areas (IUCN category \leq IV) often function as vital buffer zones to protected areas in eastern and southern Africa, and usually allow some kind of consumptive use of natural resources within their boundaries. Permitting human exploitation of wildlife within these areas is often used to provide incentives for conservation to local residents (Western et al., 1994; Lewis and Alpert, 1997).

In recent years, the importance of implementing behavioural studies in conservation biology has been widely acknowledged (Caro, 1998; Sutherland, 1998; Gosling and Sutherland, 2000), and there has been an increasing focus on how human exploitation affects wildlife populations in terms of behaviour as well as population biology. Several studies indicate that exploitation of wildlife alter population densities and population dynamics (Caro, 1999a; Fischer and Linsenmair, 2001; Milner-Gulland et al., 2001). Furthermore, because many hunters target males, demography changes in terms of female biased sex ratios (Milner-Gulland et al., 2001; Fischer and Linsenmair, 2002), which may negatively affect wildlife population dynamics (Ginsberg and Milner-Gulland, 1994; Solberg et al., 2002).

A number of studies show that anti-predator and other behaviour patterns of animals subject to human exploitation differ from those that are not hunted (Kilgo et al., 1998; de Boer et al., 2004; Donadio and Buskirk, 2006). For example, some studies suggest that animals aggregate into larger groups as an anti-predator strategy (Berger et al., 1983; Lingle, 2001), although when faced with human hunting this may not be the case (Gude et al., 2006). Moreover, animal wariness is related to the degree of hunting that population's experience. Several studies have used flight initiation distance (FID, i.e. the distance between the approaching testperson and the animal(s) at which the animal(s) initiate(s) flight) as an indirect assessment of exploitation levels. Animals generally become more wary and show a greater FID in areas with high hunting pressure (e.g. moose (*Alces alces*); Altmann, 1958; caribou (*Rangifer tarandus*); Aastrup, 2000; roe deer (*Capreolus capreolus*); de Boer et al., 2004). Changes in behaviour may have damaging effects on food intake and reproductive rates, with animals trading off the benefits of reduced predation risk against the costs of reduced foraging time or access to high-quality food resources (FitzGibbon and Lazarus, 1995; Frid and Dill, 2002; Blumstein et al., 2005).

In this study, we used impala (*Aepycerus melampus*), which is a common and widely distributed ungulate throughout the African woodlands (Jarman and Sinclair, 1979), as a model species to investigate if density, demography and behaviour of wildlife populations can be used as indicators of human exploitation, where we use a strictly protected area (i.e. National Park) as a comparison to partially protected areas (i.e. two Game Reserves and one Open Area). Illegal bushmeat hunting of resident and migratory wildlife in the Serengeti National Park (SNP) is an issue of concern for protected area managers, and has earlier reduced populations of resident herbivores, especially along the western edge of the SNP. The western side of the SNP is inhabited by a rapidly increasing human population (>1.3 million people), which exerts severe pressure on the protected areas, and where local people actively engage in illegal bushmeat hunting. The main hunt-

ing method is the use of unselective wire snares, but also more active methods are used to kill wildlife (Campbell and Hofer, 1995; Hofer et al., 1996; Holmern et al., 2006). In addition, both legal resident hunting and trophy hunting is conducted in the partially protected areas where impala is an important game species. We specifically tested whether impala populations would have (1) a lower density; (2) a larger group size; (3) a more female skewed sex ratio and (4) a more flighty behaviour towards an approaching human in the partially protected areas in comparison to the SNP.

2. Methods

2.1. Study area

The study was conducted in Serengeti National Park (14,763 km²) and in immediately adjoining partially protected areas; Grumeti Game Reserve (ca. 400 km²), Ikorongo Game Reserve (ca. 600 km²) and Ikoma Open Area (ca. 600 km²), in north-western Tanzania (Fig. 1). The study was carried out between July and December 2003, which encompass the end of the long dry season and beginning of the short rains, starting in late November.

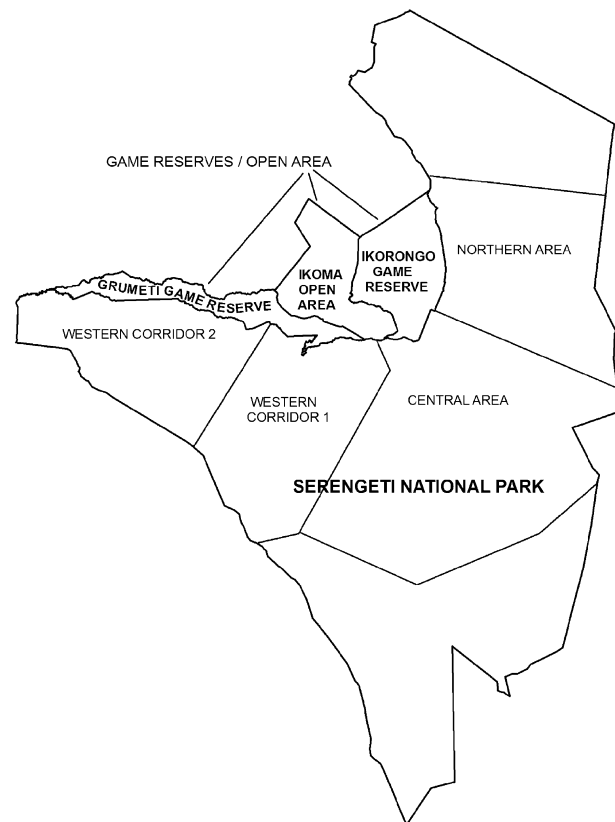


Fig. 1 – The study area showing the location of Serengeti National Park, Grumeti and Ikorongo Game Reserves and Ikoma Open Area. The five areas which were compared in the analysis; Western Corridor 1, Western Corridor 2, Central Area, Northern Area and Game Reserves/Open Area, are also shown.

In SNP no settlements, hunting, cultivation, livestock, bee-keeping, fishing or timber extraction are permitted. The most severely affected areas from illegal hunting inside the Park are in the north-west and parts of the western corridor (Hofer et al., 1996). The illegal bushmeat hunting is largely done on foot which is least conspicuous to patrolling rangers. The same legal restrictions as in the SNP apply for the Grumeti and Ikorongo Game Reserves, except that licensed tourist hunting and game cropping is allowed in the hunting season (from 1st of July until 31st December). In Ikoma Open Area settlement, cattle grazing, beekeeping, some cultivation, firewood collection and game cropping are allowed. Licensed tourist- and legal resident-hunting is conducted from cars in the hunting season, and both tourist and resident hunters are only allowed to shoot males. In addition, the partially protected areas are subject to a high illegal bushmeat hunting pressure (Hofer et al., 1996; Holmern et al., 2002).

2.2. Transects

We applied distance sampling to determine impala densities. Transects were driven on a monthly basis, covering a total distance of 2050 km. By using this approach it is possible to obtain unbiased estimates of animal densities if certain assumptions are met, namely; (1) animals on the line (i.e. road) are always detected; (2) all animals are detected in their initial locations and (3) all measurements are correctly recorded (Buckland et al., 2001). We drove a landrover at 10–20 km/h, and number of observers was 3 at all times. We used existing roads because cutting new roads were not permitted, and driving cross-country was impossible due to dense vegetation and rugged terrain. We started transects at 7.00 am and ended approx 5.00–6.00 pm. In addition, we drove transects alternately backwards and forwards, to take into account the change in animal behaviour during the day. During each transect, we took records of impala within a maximum distance of 1 km, depending on visibility, on each side of the road.

When a group or singleton was sighted, the car immediately halted and we recorded the UTM-position of the car, the distance to the animal(s) with a rangefinder and the total number of individuals. If the object was a cluster of animals, the distance was defined to represent the line from the observers to the estimated middle of the animal group. Then we measured the angle of the road and the angle of the straight line between the observers and the object, relative to true north, with the rangefinder's internal compass. These measurements allow the computation of the perpendicular distance from the object to the line. This basic information was used with the Distance software (Buckland et al., 2001) to fit detection functions that determined the density of impala per area and habitat type. The fitted detection function reflects both the decrease in detectability with distance and the lower proportion of animals that are potentially detectable (Buckland et al., 2001).

In addition, we recorded age (adult, subadult and calf) and sex classes, their initial behaviour when discovered and habitat. If it was not possible to ascertain age and sex for all animals in the group, we recorded it as unknown. Behaviour was recorded as resting, feeding, moving, vigilant, watching the

observer or fleeing. If it was a cluster with more than one animal, we recorded the behaviour of the majority of the animals. An animal was defined as vigilant when it lifted its head away from the ground and paid attention to its surroundings (Hunter and Skinner, 1998). Habitat was categorized into three types of woodland (defined as trees with canopy cover >20%) dependent on canopy cover (>70%, 50–69%, 20–49%), bushland (dense woody vegetation < 6 m in height), bushed grassland (grassland with 2–20% bush canopy), wooded grassland (grassland with 2–20% tree cover), or grassland (grass dominated) (see Kikula, 1980; Caro, 1999a). When analysing flight initiation distance we defined open vegetation to include bushed grassland and wooded grassland, and scored all other habitats as closed vegetation, because of low sample sizes.

2.3. Anti-predator behaviour

We collected separate data on flight initiation distance by driving on both existing tracks and roads covering large areas inside and outside the National Park. We were two observers at all times in the car, with the same test person in all experiments. Records were taken between 6.30 am and 6.30 pm. To avoid sampling the same individual more than once, we never covered an area more than once a week. Resident singletons or groups of animals recognized were avoided in areas previously covered.

When a suitable group or singleton was sighted, we stopped the car and turned off the engine immediately. We recorded the distance (i.e. starting distance, STD) and angle to the animals using a rangefinder, as well as scoring the individuals as alert or not alert prior to the start of the approach. A total of 226 experiments were conducted, but in 50 cases the selected animals fled before the approach commenced. These were scored as “reaction to car”. Individuals were considered as a group if they were within 5 m of each other, and other species or impalas not participating in the experiment had to be at least 50 m away. Before a new experiment was initiated, the new test group or individual had to be out of visual and olfactory contact with the former. We conducted trials according to guidelines in Caro (1986).

After recording these observations, the test person carefully opened the car door, and started to walk at a constant speed in a direct line towards the animals. When the animals fled, usually all at once and in the same direction, the test person stopped walking instantly. The observer in the car then recorded the distance to the test person. The flight initiation distance (FID) is therefore the difference between the STD and the distance to the test person when the approach was terminated.

2.4. Statistical analyses

Distance 3.5 (Buckland et al., 2001) was used to calculate density estimates for certain areas and habitat types. To avoid unnecessarily increase of the sampling variance and to minimize the number of parameters necessary to model the data with series expansions, we removed obvious outliers. A reasonable preliminary model was fitted to the data and the distance corresponding to a value of 0.15 of the probability

distribution was calculated and used as the truncation point for further analysis. We fitted all data to the following key functions; uniform, half-normal, negative exponential and hazard-rate. The hazard-rate global detection function was used in both tests to fit the dataset, and the relative fit of alternative models was evaluated using the Akaike's Information Criterion (AIC) (Sakamoto et al., 1986; Hurvich and Tsai, 1995). The densities were found to be statistically different if the confidence intervals did not overlap.

The study area was grouped into five areas in order to study differences between areas with various human activities (Fig. 1). The Serengeti National Park (SNP) was divided into 4 areas; Central Area (CA), Northern Area (NA), Western Corridor 1 (WC1) and Western Corridor 2 (WC2), whereas Grumeti and Ikorongo Game Reserves and Ikoma Open Area were pooled because the number of observations made from these areas was low. The latter is from here on referred to as Game Reserves/Open Area (GR/OA).

We used analysis of covariance (ANCOVA) to investigate which factors affected FID. We used the recent review of Stankowich and Blumstein (2005) to select the most relevant predictor variables for FID. The selected predictor variables for FID were (1) whether or not the focal individual was alert prior to the initiation of approach (alert); (2) area (inside or outside SNP); (3) vegetation structure (open or closed vegetation); (4) group size; (5) group type (single males, bachelor, female or mixed); (6) STD. Because we had a large number of possible interactions we chose to select a subset of interactions that would test our predictions about human exploitation. The interactions that were included were: starting distance \times area, starting distance \times alert, starting distance \times vegetation and area \times alert. We selected the most parsimonious model according to AIC_c (Akaike Information Criterion corrected for small samples) (Burnham and Anderson, 2002). In the analysis FID, STD and the group size was square root transformed to improve normality and reduce skewness. Chi-square tests were performed to test frequencies, a Student t-test was used to test for differences in STD between animals, and a non-parametric Kruskal-Wallis test was used to test for differences in group size between the study areas. 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. Density and demography

A statistically significant lower density in GR/OA compared to all areas inside the SNP was found (Fig. 2). Inside the SNP, the density was significantly higher in WC1 compared to WC2. The density was more than twice as high in WC1 compared to NA, but not significantly so. The density in CA was clearly higher than both NA and WC2, although not significantly higher.

The density of animals per habitat type was significantly higher inside the SNP compared to GR/OA for all habitats (Fig. 3). No observations were made for grassland in GR/OA.

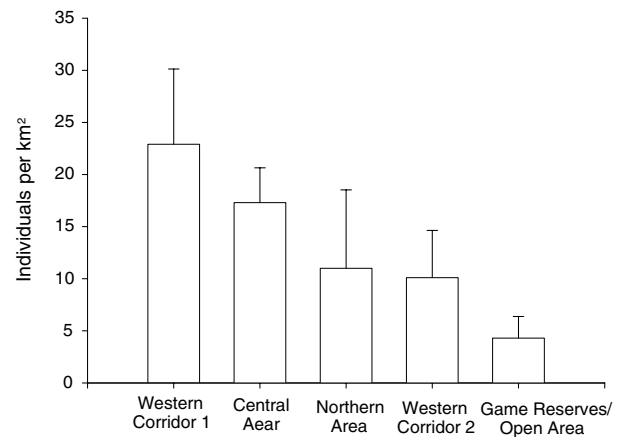


Fig. 2 – Estimated impala densities in the five areas; WC1 (N = 148), CA (N = 431), NA (N = 42), WC2 (N = 82) and GR/OA (N = 62). Ninety-five percent confidence interval is included for each estimate.

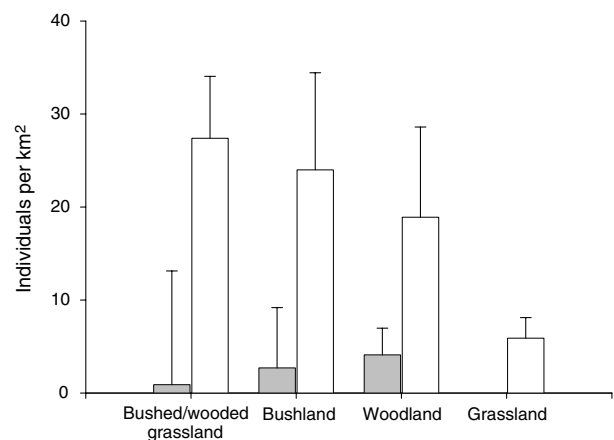


Fig. 3 – Estimated impala densities per habitat type in SNP (N = 703) and GR/OA (N = 62). Grey and white bars represent GR/OA and SNP, respectively. Ninety-five percent of confidence interval is included for each estimate.

No significant difference in group size was found between the GR/OA and the four areas (WC1, WC2, CA, NA) inside the SNP (K-W $\chi^2 = 1.84$, $df = 4$, $P = 0.765$, Table 1). Furthermore, the frequencies of different group sizes in SNP compared to GR/OA were not significantly different ($\chi^2 = 0.788$, $df = 8$, $P = 0.518$).

The sex ratio was found to be skewed towards females in all areas, and it differed significantly from a ratio of 1:1 (CA: $\chi^2 = 121.9$, $df = 1$, $P < 0.001$, WC1: $\chi^2 = 43.2$, $df = 1$, $P < 0.001$, WC2: $\chi^2 = 19.8$, $df = 1$, $P < 0.001$, NA: $\chi^2 = 15.9$, $df = 1$, $P < 0.001$, GR/OA: $\chi^2 = 15.4$, $df = 1$, $P < 0.001$). However, there was a statistically significant difference in sex ratios between the areas ($\chi^2 = 13.0$, $df = 4$, $P = 0.011$, Table 1). The sex ratio was significantly more skewed towards females in both GR/OA ($\chi^2 = 7.6$, $df = 1$, $P = 0.006$) and NA ($\chi^2 = 4.7$, $df = 1$, $P = 0.018$) compared to CA. In addition, the sex ratio was also significantly more skewed towards females in GR/OA compared to WC1 ($\chi^2 = 4.2$, $df = 1$, $P = 0.039$).

Table 1 – Mean group size ± standard error (SE) and sex ratio (adult male+ subadult male: adult female + subadult female) for impala seen in the five different areas; CA, WC1, WC2, NA and GR/OA

Area	N	Mean group size ± SE	Sex-ratio (M:F)
Central area	442	10.3 ± 0.7	1:1.6
Western Corridor 1	151	12.0 ± 1.3	1:1.7
Western Corridor 2	92	9.6 ± 1.3	1:1.8
Northern Area	45	11.7 ± 2.3	1:2.0
Game Reserves/Open Area	62	9.2 ± 1.3	1:2.1

Number of observations is included.

3.2. Behaviour

3.2.1. Behaviour along transects

Fig. 4 indicates the behaviour immediately after the animals were detected during transects. There was a statistical significant difference in this initial behaviour between the SNP and

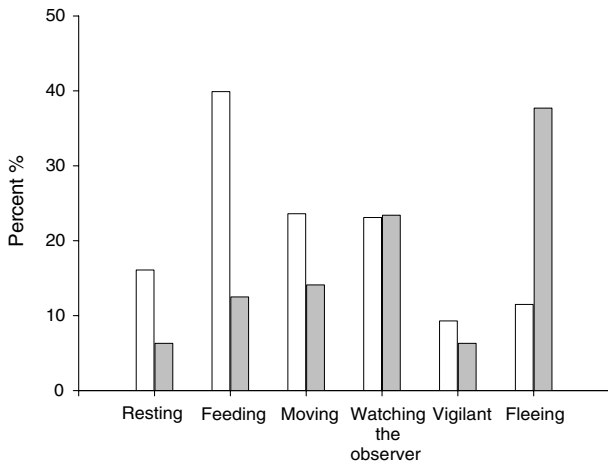


Fig. 4 – Frequency of the different initial behaviours of impala during transects in SNP (N = 725) and GR/OA (N = 65). Grey and white bars represent GR/OA and SNP, respectively.

GR/OA ($\chi^2 = 90.3$, $df = 20$, $P < 0.001$). In the GR/OA 39% of the animals fled when the car stopped, compared to only a mean of 7% in the areas inside the SNP. Furthermore, 3% and 13% of the animals in GR/OA were resting and feeding, respectively, compared to a mean of 15% and 36%, respectively in the areas inside the SNP.

3.2.2. Flight initiation distance

Inside the SNP a total of 170 trials were conducted and in 12.4% of these cases the impalas fled as a reaction to the presence of the car before the human approach could start (after the car had stopped while recording initial measurements). In the GR/OA ($n = 56$) 51.8% of the impalas fled as a reaction to the presence of the car, a difference which was significant ($\chi^2 = 38.0$, $df = 1$, $P < 0.001$). However, the STD was not different between animals reacting to the car and those used in the approaches ($t = 1.59$, $df = 224$, $P = 0.111$), but the STD outside the SNP was significantly larger than inside for those that reacted to the car ($t = -4.13$, $df = 48$, $P < 0.001$). For the trials where approaches were done and where we had a complete dataset ($N = 170$) the most parsimonious ANCOVA model for FID included the terms: STD, area, alert and the interactions $STD \times area$, and $alert \times area$ (Table 2, Table 3; adjusted $R^2 = 0.76$, $P < 0.0001$). However, when we excluded STD this model only explained 15% (adjusted $R^2 = 0.15$, $P < 0.0001$) of the observed variation in FID. It is clear that FID is influenced to a large extent by STD, and that FID increased in the areas

Table 3 – Estimates for the most parsimonious model of flight initiation distance (FID), for further details see Table 2

Coefficients	Estimate	SE	t	P
Intercept	0.96	0.38	2.54	0.012
STD	0.75	0.04	18.96	<0.001
Alert	0.54	0.16	3.41	<0.001
Area	2.88	0.83	3.48	<0.001
STD × Area	-0.22	0.07	-3.17	0.002
Alert × Area	-0.83	0.41	-2.03	0.044

Table 2 – Set of the nine most parsimonious and global ANCOVA model with flight initiation distance (FID) as dependent variable

Model	K	R ²	AIC _c	ΔAIC _c	ω _i
STD + alert + area + STD × area + alert × area	7	0.760	471.1	0	0.158
STD + alert + area + vegetation + STD × area + alert × area + STD × vegetation	9	0.762	472.0	0.83	0.103
STD + alert + area + group size + STD × area + alert × area	8	0.759	472.6	1.47	0.076
STD + alert + area + vegetation + STD × area + STD × vegetation	8	0.759	472.7	1.55	0.072
STD + alert + area + STD × area + alert × area + alert × STD	8	0.759	472.9	1.78	0.065
STD + alert + area + vegetation + group size + STD × area + alert × area + STD × vegetation	10	0.763	473.1	1.97	0.058
STD + alert + area + STD × area	6	0.756	473.2	2.06	0.056
STD + alert + area + vegetation + group size + STD × area + STD × vegetation	9	0.759	473.9	2.78	0.039
STD + alert + area + group type + STD × area + alert × area	8	0.760	474.5	3.34	0.029
STD + alert + area + vegetation + group size + group type + STD × area + alert × area + STD × vegetation + STD × alert	12	0.761	479.1	7.95	0.002

The models were ranked by the corrected Akaike Information Criterion corrected for small samples (AIC_c). (K = number of parameters; ΔAIC_c = difference in AIC_c between the best and the actual model; ω_i = Akaike's weights, i.e. normalized likelihoods of the models). The most parsimonious model is on the top of the list.

outside the SNP. The predictor variable vegetation was included in the second best model, although there was a low evidence ratio (ω_1/ω_2) between the two (1.53), it included more parameters and therefore was not the most parsimonious model. But there was no clear support for any of the first best models (Table 2). Group type was not included among the best models.

4. Discussion

The partially protected areas contained lower densities of impala than all areas inside the SNP, which are in accordance with several case studies from similar areas in Africa (Hofer et al., 1996; Verlinden, 1997; Caro, 1999a). Due to the fact that the data collection was carried out only during the dry season, we cannot rule out the possibility that some of the density differences can be caused by the animals' seasonal movements between habitats (Jarman and Sinclair, 1979). However, there is no reason to believe that habitat differences, in respect to quality or structure, between the partially protected areas and the SNP could cause the density differences. The partially protected areas contain similar habitat types as in the SNP, and should be equally suitable for impala (Herlocker, 1976). Moreover, the woodland, bushland and wooded/bushed grassland habitats that were highly preferred by impala inside the SNP contained much lower densities outside the SNP. Grassland was not represented outside the SNP, but will only have a minor effect on the results since this habitat type is less preferred by impala. This suggests that human exploitation played a central role in producing low impala densities outside the SNP, as well as in areas within the SNP. Earlier studies show that the most severely affected areas from illegal hunting are in the north-west and western part of the Western Corridor (Campbell and Hofer, 1995; Hofer et al., 1996), and this concurs with our results that WC2 and NA had lower densities than the other areas inside the SNP.

No significant difference was found in the group size in any of the areas. In addition, the representation of various group sizes in the areas was not significantly different, which can rule out the possibility that a larger portion of single males in one area would affect mean group size. Similar results have also been found in other areas for impala (Hunter and Skinner, 1998; Caro, 1999b). Creel and Winnie (2005) reported that for elk (*Cervus elaphus*), aggregation is likely to be a foraging response that occurs when the risk of predation is low combined with higher availability of resources in some areas. Similarly, Jarman and Jarman (1979) found that group size of impala in SNP was smaller during the dry season than during the wet season, which might indicate that group size is influenced more by resource availability (see also Berger et al., 1983; Creel and Winnie, 2005).

The sex ratio was found to be female biased in the whole study area. This is expected in nature due to a higher mortality rate among males, caused by higher predation risk and competition between males (FitzGibbon and Lazarus, 1995). However, the sex ratio was more skewed towards females in GR/OA than all areas inside the SNP, which indicate a higher male mortality rate here. The result however, was only significant for GR/OA vs. CA and WC1. This may indicate that there is more skew towards females in the partially protected areas

and in areas inside the SNP more subjected to illegal hunting (Hofer et al., 1996). Despite that wire snaring is the most prevalent hunting method in the SNP, results reported by Holmern et al. (2006) suggest that illegal hunting has a male bias in kills. In addition, a contributing factor might be that both resident and tourist hunters target males. However, quotas are low and should not affect sex ratios if they are followed, but the low level of law enforcement outside the SNP implies that these are mere conservative lower estimates of offtake levels (Holmern et al., 2004).

Increased disturbance levels might also have indirect effects on animal survival. The increased energy expenditure associated with flight and higher alertness levels might have serious effects for the physical condition of animals. For example, a model exploring the cost of human disturbance found large reductions in the number of food items captured following disturbance (Blumstein et al., 2005). High hunting pressure in some areas might cause animals to shift to more protected habitats, which may be of lower quality or have a higher risk of predation (Kilgo et al., 1998). Our results indicate that outside the SNP, impalas are more flighty and avoid open areas which are more exposed to human hunters (Fig. 3). Similar findings where animals are more wary in exploited areas have been reported in other studies (e.g. Caro, 1999b; Donadio and Buskirk, 2006).

We found a clear influence of hunting pressure on FID. This supports findings of Matson et al. (2005) who also found that impalas have a longer FID in hunted areas. Longer FID in areas experiencing high hunting activity has also been reported by other studies (Altmann, 1958; de Boer et al., 2004). We also find less support of an effect of group size and group type on FID. However, de Boer et al. (2004) reported that larger groups in roe deer and fallow deer (*Dama dama*) had a greater flight distance than small groups or single individuals. Likewise, Aastrup (2000) reported similar results for caribou. In contrast, Matson et al. (2005) found greater FIDs for small groups of impala. Recarte et al. (1998) reported that female fallow deer were more vigilant than males, but de Boer et al. (2004) found no such effect on flight distance of roe deer and fallow deer. Such sex differences in risk assessment might reflect presence of young, but might also be related to human hunting.

5. Conclusions

Our results indicate that several characteristics in the impala population are clearly altered in areas subjected to human exploitation, which have implications for conservation and management. The present illegal bushmeat hunting combined with unregulated legal hunting in the study area are most likely the cause of the observed differences, and questions whether managers of partially protected areas have adequate resources to meet conservation goals (Hofer et al., 1996; Caro et al., 2000). Besides causing reductions in density, illegal hunting causes changes in demography and behaviour that may have the potential to affect population growth rates. Although we found support for that demography and behaviour can be used as indicators of exploitation, it is likely to be dependent on hunting pressure and hunting mode. However, impala is only one of several ungulates targeted by illegal

hunters, and it could therefore be expected that the results obtained in this study might reflect the state of other ungulates in and around the SNP. This is cause for serious concern, and is a matter that needs further attention.

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REFERENCES

- Aastrup, P., 2000. Responses of west Greenland caribou to the approach of humans on foot. *Polar Research* 19, 83–90.
- Altmann, M., 1958. The flight distance in free ranging big game. *Journal of Wildlife Management* 22, 207–209.
- Berger, J., Daneke, D., Johnson, J., Berwick, S.H., 1983. Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. *Biological Conservation* 25, 193–208.
- Blumstein, D.T., Fernández-juricic, E., Zollner, P.A., Garity, S.C., 2005. Interspecific variation in anti-predator behaviour and human-wildlife coexistence. *Journal of Applied Ecology* 42, 943–953.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. *Introduction to Distance Sampling – Estimating the Abundance of Biological Populations*. Oxford University Press, New York.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer, Berlin.
- Campbell, K., Hofer, H., 1995. People and wildlife: spatial dynamics and zones of interaction. In: Sinclair, A.R.E., Arcese, P. (Eds.), *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem*. The University of Chicago Press, Chicago and London, pp. 534–570.
- Caro, T.M., 1986. Ungulate antipredator behaviour: preliminary and comparative data from African bovids. *Behaviour* 128, 189–228.
- Caro, T.M., 1998. *Behavioural Ecology and Conservation Biology*, first ed. Oxford University Press, New York and Oxford.
- Caro, T.M., 1999a. Densities of mammals in partially protected areas: the Katavi ecosystem of western Tanzania. *Journal of Applied Ecology* 36, 205–217.
- Caro, T.M., 1999b. Demography and behaviour of African mammals subject to exploitation. *Biological Conservation* 91, 91–97.
- Caro, T.M., Rejmánek, M., Pelkey, N., 2000. Which mammals benefit from protection in east Africa. In: Entwistle, A., Dunstone, N. (Eds.), *Priorities for the Conservation of Mammalian Diversity*. Cambridge University Press, Cambridge, pp. 221–227.
- Creel, S., Winnie, J.A., 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour* 69, 1181–1189.
- de Boer, H.Y., van Breukelen, L., Hootsmans, M.J.M., van Wieren, S.E., 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. *Wildlife Biology* 10, 35–41.
- Donadio, E., Buskirk, S.W., 2006. Flight behaviour in guanacos and vicunas in areas with and without poaching in western Argentina. *Biological Conservation* 127, 139–145.
- Fischer, F., Linsenmair, K.E., 2001. Decreases in ungulate population densities. Examples from the Comoe National Park, Ivory Coast. *Biological Conservation* 101, 131–135.
- Fischer, F., Linsenmair, K.E., 2002. Demography of a West African kob *Kobus kob* population. *African Journal of Ecology* 40, 130–137.
- FitzGibbon, C.D., Lazarus, J., 1995. Antipredator behaviour of Serengeti ungulates: individual differences and population consequences. In: Sinclair, A.R.E., Arcese, P. (Eds.), *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem*. The University of Chicago Press, Chicago and London, pp. 274–296.
- Frid, A., Dill, L.M., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6, 11–35.
- Ginsberg, J.R., Milner-Gulland, E.J., 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. *Conservation Biology* 8, 157–166.
- Gosling, L.M., Sutherland, W.J., 2000. *Behaviour and Conservation*. Cambridge University Press, New York.
- Gude, J.A., Garrott, R.A., Borkowski, J.J., King, F., 2006. Prey risk allocation in a grazing ecosystem. *Ecological Applications* 16, 285–298.
- Herlocker, D., 1976. *Woody Vegetation of the Serengeti National Park*. College Station. Texas A and M University, Texas.
- Hofer, H., Campbell, K.L.I., East, M.L., Huish, S.A., 1996. The impact of game meat hunting on target and non-target species in the Serengeti. In: Taylor, J., Dunstone, N. (Eds.), *The Exploitation of Mammal Populations*. Chapman and Hall, London, pp. 117–146.
- Holmern, T., Røskaft, E., Mbaruka, J., Mkama, S.Y., Muya, J., 2002. Uneconomical game cropping in a community-based conservation project outside the Serengeti National Park, Tanzania. *Oryx* 36, 364–372.
- Holmern, T., Johannesen, A.B., Mbaruka, J., Mkama, S., Muya, J., Røskaft, E., 2004. Human-wildlife conflicts and hunting in the Western Serengeti, Tanzania. NINA Report 26. Norwegian Institute for Nature Research, Trondheim, Norway.
- Holmern, T., Mkama, S.Y., Muya, J., Røskaft, E., 2006. Intraspecific prey choice of bushmeat hunters outside the Serengeti National Park, Tanzania: a preliminary analysis. *African Zoology* 41, 81–87.
- Hunter, L.T.B., Skinner, J.D., 1998. Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135, 195–211.
- Hurvich, C.M., Tsai, C.L., 1995. Model selection for extended quasi-likelihood models in small samples. *Biometrics* 51, 1077–1084.
- Jarman, P.J., Jarman, M.V., 1979. The dynamics of ungulate social organization. In: Sinclair, A.R.E., Norton-Griffiths, M. (Eds.), *Serengeti – Dynamics of an Ecosystem*. The University of Chicago Press, Chicago and London, pp. 185–220.
- Jarman, P.J., Sinclair, A.R.E., 1979. Feeding strategy and the pattern of resource partitioning in ungulates. In: Sinclair, A.R.E., Norton-Griffiths, M. (Eds.), *Serengeti – Dynamics of an Ecosystem*. The University of Chicago Press, Chicago and London, pp. 130–163.

- Kikula, I.S., 1980. Landsat satellite data for vegetation mapping in Tanzania: the case of the Rukwa Region. Bureau of Resource Assessment and Land Use Planning, Research Report No. 41, University of Dar es Salaam.
- Kilgo, J.C., Labisky, R.F., Fritzen, D.E., 1998. Influences of hunting on the behaviour of white-tailed deer: implications for conservation of the Florida panther. *Conservation Biology* 12, 1359–1364.
- Lewis, D.M., Alpert, P., 1997. Trophy hunting and wildlife conservation in Zambia. *Conservation Biology* 11, 59–68.
- Lingle, S., 2001. Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. *Ethology* 107, 295–314.
- Matson, T.K., Goldizen, A.W., Putland, D.A., 2005. Factors affecting vigilance and flight behaviour in impalas. *South African Journal of Wildlife Research* 35, 1–11.
- Milner-Gulland, E.J., Kholodova, M.V., Bekenov, A., Bukreeva, O.M., Grachev, A., Amgalan, L., Lushchenkina, A.A., 2001. Dramatic declines in saiga antelope populations. *Oryx* 35, 340–345.
- R Development Core Team, 2006. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Recarte, J.M., Vincent, J.P., Hewison, A.J.M., 1998. Flight responses of park fallow deer to the human observer. *Behavioural Processes* 44, 65–72.
- Sakamoto, Y., Ishiguro, M., Kitawaga, G., 1986. Akaike Information Criterion Statistics. KTK Scientific Publishers, Tokyo.
- Solberg, E.J., Loison, A., Ringsby, T.H., Sæther, B.-E., Heim, M., 2002. Biased adult sex ratio can affect fecundity in primiparous moose *Alces alces*. *Wildlife Biology* 8, 117–128.
- SPSS, 2005. SPSS for Windows. Release 14.0. SPSS Inc., Chicago, IL.
- Stankowich, T., Blumstein, D.T., 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of The Royal Society B* 272, 2627–2634.
- Sutherland, W.J., 1998. The importance of behavioural studies in conservation biology. *Animal Behaviour* 56, 801–809.
- Verlinden, A., 1997. Human settlements and wildlife distribution in the Southern Kalahari of Botswana. *Biological Conservation* 82, 129–136.
- Western, D., Wright, M., Strum, S.C., 1994. *Natural Connections: Perspectives in Community-based Conservation*. Island Press, Washington DC.

Paper IV

Margins of safety and escape responses in Thomson's gazelle

Running head: Margins of safety

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Abstract

The perceived risk is important when deciding when to flee from an approaching predator that appears threatening. This could be done by the prey either through monitoring the distance to an approaching threat or by estimating the expected time it would take the predator to arrive at their location. Animals are expected to adjust their flight initiation distance (FID), flight speed and length according to a cost-benefit trade-off. In this study, we examined flight responses (FID, flight speed and flight length) in Thomson's gazelles (*Gazella thomsoni*) in relation to different risk levels, by varying our approach speed. We found that there was no difference in FID according to approach speed, when we took starting distance into account. However, fast approaches elicited higher flight speeds, but had no effect on flight length. In addition, we found that gazelles appeared to display their escape capabilities through condition dependent signals when the perceived threat was high. Our results provide support for the hypothesis that gazelles maintain a spatial margin of safety. Moreover, Thomson's gazelles show a great flexibility in their flight responses, and alarm signals may convey important clues on the perceived level of predation risk.

Keywords: antipredator behaviour, flight initiation distance, Serengeti, starting distance, Thomson's gazelle

Introduction

Fleeing is a common antipredator behaviour among animals when confronted with a potentially dangerous predator. The distance between an approaching predator and prey at which escape commences is usually referred to as flight initiation distance (FID) or flush distance (but also approach distance) (Ydenberg and Dill 1986). Given a history of persecution, animals will react to approaching humans in the same way as they would towards predators. Therefore humans are often used as a standardized stimulus when measuring FID and other flight responses (Frid and Dill 2002; Blumstein 2003; Stankowich and Blumstein 2005).

According to Ydenberg and Dill (1986), FID should be optimised rather than maximised. Animals should therefore minimize the cost of escape by not moving away from the predator until the cost of remaining (i.e. potentially being killed) exceeds the cost of escaping (i.e. terminating current behaviour, locomotion costs). Consequently, escape decisions based on the animal's current assessment risk will vary dynamically. Several studies show that animals adjust their FID as a function of perceived risk. For example, in gray squirrels (*Sciurus carolinensis*) Dill and Houtman (1989) showed an effect on FID of distance from the closest refuge tree, while Bonenfant and Kramer (1996) found that woodchucks (*Marmota mona*) have greater FIDs when farther from their burrow. Similarly, Diego-Rasilla (2003) reported that wall lizards (*Podarcis muralis*) had a greater FID in areas experiencing higher predation pressure.

There are few studies that have explicitly investigated the underlying mechanisms of risk assessment. Stankowich and Blumstein (2005) showed that there is considerable contention on how prey use margins of safety in relation to predation risk. Of the studies examined, nine out of 15 found an effect on the prey's FID in relation to the predator approach speed. This indicates that prey might monitor time to arrival of the predator, when deciding to flee, since a predator moving at high speed will use less time to reach the prey and therefore pose a greater imminent threat to the animal's survival. For instance, Walther (1969) reported that Thomson's gazelles (*Gazella*

thomsoni) flee at greater distances in response to a running hyena (*Crocuta crocuta*) than to a walking hyena. For Columbian black-tailed deer (*Odocoileus hemionus columbianus*), Stankowich and Coss (2005) found that animals have larger FIDs during rapid human approaches. Similarly, FID has been reported to increase with predator approach speed for broad-headed skinks (*Eumeces laticeps*), desert iguanas (*Dipsosaurus dorsalis*) and Bonaire whiptail lizards (*Cnemidophorus murinus*) (Cooper 1997, 2003; Cooper et al. 2003). Temporal assessment of risk was also suggested by Dill (1990) for explaining escape responses to an approaching object by African cichlid fish (*Melanochromis chipokae*), where cichlids appeared to regulate primarily FID rather than flight speed in order to reach refuge in time.

On the other hand, some studies indicate that prey might instead evaluate the distance between themselves and an approaching predator and use it as a cue for the time to escape. Maintaining such a spatial margin of safety might be a more conservative strategy to adopt, because in order to calculate the time of arrival of a predator (i.e. using a temporal margin of safety) the prey must estimate the speed of the predator and assume that it will remain constant, which might be more prone to error (Cardenas et al. 2005). Accordingly, Bonenfant and Kramer (1996) reported that in woodchucks there was a lack of effect of approach speed on FID, as well as on flight speed, and suggested that woodchucks therefore maintained a spatial margin of safety. Cardenas et al. (2005) also found that in galahs (*Cacatua roseicapilla*) FID did not change in response to varying approach speed, which also suggests that some species may use distance for risk assessment.

Thus, in order to evaluate risk perception in Thomson's gazelles we conducted experimental human approaches towards individual gazelles, where we in contrast to the early study of Walther (1969), explicitly recognised the importance of starting distance of the predator. We tested the prediction if FID of the prey increased with increasing approach speed in accordance with a temporal margin of safety perception of risk level. Moreover, the length of the flight and flight speed should also reflect trade offs between costs and benefits (Ydenberg and Dill 1986). However,

there are up to now very few studies that have focused on these flight responses. Recently, Cooper et al. (2006) showed that in Balearic lizards (*Podarcis lilfordi*) increased opportunity costs (i.e. more food at feeding site) led to shorter flight length when approached by a human. Whereas, Martín and López (1996) reported that the distance fled by the lacertid lizard (*Psammmodromus algirus*) was greater when the predator approached more rapidly, this was not the case in broad-headed skinks (Cooper 1997). We therefore investigated the effect of approach speed on flight length and flight speed where we predicted that flight length and flight speed would be greater when the threat level was perceived as higher.

Methods

Location and subject

We studied Thomson's gazelles who are small migratory grazers (ca. 20 kg), between August to mid December 2003 in Serengeti National Park (SNP), northern Tanzania. Human approaches were conducted on single adult males located in open vegetation (grassland or wooded grasslands with 2-20 % tree cover) with short grass (< 30 cm) inside the SNP between 06:00 AM and 07:00 PM. We selected single male individuals to easier and more accurately monitor escape responses, since they were mostly located on the periphery of large Thomson's gazelle herds. We also excluded the areas around Seronera headquarters and along the Seronera River which have a high frequency of tourist vehicles to reduce possible habituation effects on the Thomson's gazelles. According to Runyan and Blumstein (2004), a modest extent of pseudoreplication do not influence results in FID studies, but in order to minimise this potential problem we never resampled an area before at least a week had gone by, and made a conscious effort to avoid territorial males used in previous trials. There are several carnivores that predate on Thomson's gazelles, the most common among these are lions (*Panthera leo*), leopards (*Panthera pardus*), hyenas, cheetahs (*Acinonyx jubatus*), and jackals (*Canis adustus*, *C. aureus*, *C. mesomelas*). Inside the SNP, all consumptive activities are strictly

prohibited and humans are only allowed to move around in vehicles. Despite these regulations, illegal bushmeat hunting is still a widespread activity (wire snares are most commonly used), but Thomson's gazelle appears to be less affected than other herbivore species (Arcese et al. 1995, but see Holmern et al. 2006).

Experimental procedures

The individual selected for an approach had to be at least 50 m from other individuals or groups (including individuals from other large mammal species) and have a clear line of sight to the starting point of the approach. Moreover, the individual chosen had to be closer to the vehicle than other individuals around it (along the line of approach), so that its behaviour was not affected by other individual's reactions to the approach. When a suitable individual had been identified from the road, we stopped and switched off the car engine. We noted initial behaviour of the individual before commencing the approach, where individuals were scored as alert if they were standing with ears erect and facing the vehicle, whereas other behaviours were scored as not alert. Approaches were not conducted if a potential predator was in sight, another vehicle was nearby, if it was raining, or if individuals had visual contact with earlier trials. Approaches were abandoned if the individual suddenly changed its behaviour due to disturbances other than the approaching human.

Before we began the approach we measured the distance to the individual (starting distance, STD) with a Leica geovid 7 x 42 BDA rangefinder, which was accurate to the nearest 1 m (< 366 m) (with an integrated electronic compass). Whereupon, the testperson (T.H. 1.90 m tall male, wearing neutral coloured cloths) started walking in a slow steady pace (hereafter, "slow" approaches, $n = 103$) directly towards the individual (mean \pm SD, 1.7 ± 0.2 m/s (1 SE), $n = 10$ test speed trials). Immediately, when the individual took flight, the testperson stopped the approach and using a stopwatch kept track of the time the individual used to run away before stopping again (Flight time = FT). After the approach had been terminated the second observer (driver) recorded

the distance to the testperson and the distance to where the animal had terminated its flight (Stop distance, STOPD). Thereafter, the angles in regards to true north of the original start (angle 1) – and stop position (angle 2) of the gazelle was noted from outside the vehicle. Thus the angle α was the difference between the two above mentioned angles ($|\text{angle } \alpha| = \text{angle 1} - \text{angle 2}$), where we transformed angle α into radians for further use. Flight length (FL) was calculated using the equation: $FL = \sqrt{(\text{STD})^2 + (\text{STOPD})^2 - (2 \times \text{STD} \times \text{STOPD} \times \cos(\alpha))}$. Whereas flight speed (FS) was estimated as: FL/FT . In addition, for a subset of the data we also recorded the occurrence of stotting during gazelle escapes. Stotting is defined as leaping off the ground with all four legs held stiff and straight (Walther 1969). Trials were discarded if there was any doubt about the distances and times measured. In addition to making slow walks, we (T.H.) also conducted fast approaches (hereafter, “fast” approaches, $n = 58$) (4.4 ± 0.7 m/s, $n = 10$). We restricted the data set to starting distances < 250 m for both approach types, both to ensure that the testperson would be able to maintain the required standardized speed.

Statistical analyses

Predators do not begin approaches of prey at fixed distances, and it is not surprising that starting distance strongly affects alert distances and FID, as has been shown for birds (Fernández-Juricic and Schröder 2003; Blumstein 2003). Thus, we included starting distance as an independent variable in our tests and we conducted a total of 161 trials. We used analysis of covariance (ANCOVA) to investigating the relationship of each dependent variable (FID, flight speed and flight length) with the independent variables. However, because of an unbalanced design, we restricted the analysis to individuals that displayed not-alert behaviour prior to the approach (Alert: walk, $n = 24$, fast, $n = 8$; Not alert: walk, $n = 80$, fast, $n = 49$). When testing the effect of approach speed on FID, we fitted the variables: approach speed, starting distance, and the interaction of approach speed and starting distance. For flight speed and flight length: approach speed, FID and the interaction between

approach speed and FID was used. We did not force the models through the origin (i.e. eliminating the intercept), since extrapolation outside the data range is not advisable (Neter et al. 1996; Cade and Terrell 1997). In the analysis the variables FID, flight speed, flight length and starting distance were square root transformed to improve normality of the residual errors. We performed chi-square tests to test frequencies and the considered significance value was $P < 0.05$ throughout. The analyses were done using R 2.3.0 Software (R Development Core Team 2006) and SPSS 14.0 (2005).

Results

When the animals displayed alert behaviour prior to the approach, the minimum FID was 38 m (i.e. starting distance was 43 m), but when the animal did not show alert behaviour prior to the approach, the minimum FID was 17 m (i.e. starting distance was 213 m) (Figure 1a). Among the variables included in the analysis for not alert animals, starting distance and FID, as well as flight speed and flight length were correlated (Table 1).

FID of Thomson's gazelles was affected by starting distance ($F_{1,125} = 41.53$, $P < 0.001$), but the main effect of approach speed was not significant ($F_{1,125} = 1.51$, $P = 0.222$). The interaction term between starting distance and approach speed had also no effect ($F_{1,125} = 0.03$, $P = 0.854$) (Figure 1b).

Furthermore, FID did not affect flight speed ($F_{1,125} = 2.39$, $P = 0.124$). However, the approach speed had a significant effect on flight speed ($F_{1,125} = 4.11$, $P = 0.045$), where fast approaches had a higher flight speed than slow approaches (Figure 1c). The interaction between FID and approach speed was not significant ($F_{1,125} = 0.29$, $P = 0.593$).

Likewise, FID did not affect flight length ($F_{1,125} = 0.07$, $P = 0.792$), nor did the approach speed ($F_{1,125} = 0.38$, $P = 0.540$). Neither was the interaction between FID and approach speed significant ($F_{1,125} = 1.11$, $P = 0.540$) (Figure 1d).

For a subset of the data we examined the occurrence of stotting during escapes ($n = 58$). Gazelles that displayed not alert behaviour prior to the approach, stotted significantly more often during fast approaches ($\chi^2 = 4,609$, $df = 1$, $P = 0.032$, $n = 51$), whereas gazelles that were alert prior to the approach did not show any difference in the occurrence of stotting between slow and fast approaches (Fischer's exact test, $P = 0.286$).

Discussion

Walther (1969) first studied flight behaviour in Thomson's gazelle in the Serengeti National Park by observing responses to approaching carnivores, as well as conducting approaching-experiments by using a vehicle (from a fixed starting distance). His results suggest that Thomson's gazelle appear to have predator specific responses, and that FID increases with predator approach speed and with predator group size. In contrast, after taking into account starting distance, we found no effects of the speed of the approaching predator on the FID of Thomson's gazelle's. However, approach speed had an effect on flight speed, as well as on the occurrence of stotting.

FID depends to a large extent on starting distance, where animals that detect an approaching predator will flee at a greater distance in order to reduce costs of escape. Either as proposed by Blumstein (2003) animals may do this in order to choose to avoid fleeing at maximum flight speed or after detecting a potential predator they will flee in order to minimise monitoring costs. On the other hand, at very long distances animals engaging in not alert behaviour will not detect an approaching predator until it rescans the surrounding area, and may therefore initiate flight at a sub-optimal FID.

Several studies have investigated how animals use margins of safety, but no clear pattern has yet emerged, although non-mammalian prey seem particularly responsive to increased predator speed (Cooper 1997, 2003; Cooper et al. 2003; Stankowich and Blumstein 2005). In Thomson's gazelles, FID has earlier been reported to increase in response to higher predator approach speed

(Walther 1969). In contrast, predator speed did not influence FID in our study. A few other studies have also reported the same pattern, where in Blue chromis damselfish (*Chromis cyanea*) FID was independent of the speed of a model predator (Hurley and Hartline 1974), neither was there an effect of approach speed on woodchucks (Bonenfant and Kramer 1996). Likewise, Cardenas et al. (2005) found that FID in galahs were not related to how quickly they were approached. Although the small differences between speed treatments can be invoked as a possible explanation (0.55 m/s, Bonenfant and Kramer 1996; 0.9 m/s, Cardenas et al. 2005), this study had a relatively large difference between the slow and fast approaches (2.7 m/s). Assessing speed accurately might be prone to error. Adopting a conservative strategy by assessing distance might thus incorporate the inaccuracy of the information provided, and allow animals quickly to evaluate the threat level and when to flee (Bouskila and Blumstein 1992).

Most studies investigating trade-offs in escape strategies have used FID as the main metric for responses (Stankowich and Blumstein 2005). However, a few studies have also involved other aspects of encounters, such as flight speed and flight length (Dill 1990; Bonenfant and Kramer 1996; Copper et al. 2006). For instance, in woodchucks flight speed was unrelated to FID when the woodchucks were located between the burrow and the human approacher (Bonenfant and Kramer 1996). Similarly, Dill (1990) found that flight speed was not affected by FID in cichlids. However, increased predation risk has been found to affect flight length in some species. Stone et al. (1994) found that the lava lizard (*Microlophus* sp.) in the Galapagos fled greater distances on islands where there was higher predation threat (but see Diego-Rasilla 2003). Similarly, Setsaas (2004) reported that impalas (*Aepyceros melampus*) outside the Serengeti National Park fled longer distances in areas experiencing higher hunting pressure when approached by a human. Our results show that FID did not affect flight speed or flight length in Thomson's gazelle, whereas there was an effect of approach speed on flight speed, but not on flight length.

Nevertheless, animals are dynamic in their escape responses, and our way of measuring the flight response might not have captured the full extent of their reaction. In fact, instead of maintaining an even flight speed the gazelles might have responded by a sharp non-linear or declining linear response in speed because the predator (i.e. the test person) did not pursue the individual. Such a response would not be captured by our methods since we only estimated average speed across the flight length. In addition, gazelles are unlikely to run in a straight line between two points which might lead to an underestimation of flight speed and flight length. Moreover, Thomson's gazelles have a very rapid acceleration which gives them great flexibility to adjust escape responses according to the threat level. Bonenfant and Kramer (1996) also reported that prey continuously monitor the threat represented by a pursuing predator in order to minimise its energy expenditure. Therefore it is likely that flight speed declined rapidly after the animal realised that it was not being pursued.

Our study suggests that together with keeping a flexible distance to the predator, Thomson's gazelles also use condition dependent signals when the risk level increases. Animals that were not alert prior to the approach probably had less time to assess the threat and therefore stotted in order to signal their condition, whereas the animals that were already alert had probably assessed the threat level and decided on an adequate response. A number of ungulates display different types of behaviour when fleeing (i.e. tail flagging, snorting, bounding, stotting) (Caro et al. 2004). For example, white – tailed deer (*Odocoileus virginianus*) often flag their tail when alarmed and impalas may leap to show some aspect of their physical condition to approaching predators (Caro 1986a; Caro et al. 1995). Similarly, FitzGibbon and Fanshawe (1988) reported that in Thomson's gazelles, stotting is likely to be an honest signal of their health to the predator. Thus the frequency and occurrence of stotting show the predator the capabilities that an animal has to escape before the prey has to engage in a potentially costly high speed flight (i.e. in terms of energy usage, potential injury). Accordingly, FitzGibbon and Fanshawe (1988) found that African wild dogs (*Lycaon*

pictus) pursue stotting gazelles at lower rates than they do other gazelles. Moreover stotting is also likely to be energetically costly. Caro (1986b) found a negative correlation between the frequencies of stots and flight speed during high speed pursuits by cheetahs, which suggest that stotting is costly (i.e. reduces speed and manoeuvrability). Species living in open environments may also be particularly prone to adopt visual signals, since open vegetation allows the predators to have a greater opportunity to observe the prey's evasive manoeuvres (Caro 1986b, Caro et al. 2004).

In conclusion, our results show that Thomson's gazelles are very flexible in their responses and that Thomson's gazelles appear to maintain a spatial margin of safety, together with the use of condition dependent signals. Since such signals are common among species living in open habitats, including escape responses, such as alarm signals in future studies might give an additional indication of the species' risk perception.

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References

- Arcese, P., Hando, J. & Campbell, K. L. I. 1995. Historical and present-day anti-poaching efforts in Serengeti. In: *Serengeti II: Dynamics, Management and Conservation of an Ecosystem* (Ed. by A. R. E. Sinclair & P. Arcese), pp. 506-533. Chicago, IL, USA: University of Chicago Press.
- Blumstein, D. T. 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management*, 67, 852-857.
- Bonenfant, M. & Kramer, D. L. 1996. The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behavioral Ecology*, 7, 299-303.
- Bouskila, A. & Blumstein, D. T. 1992. Rules of thumb for predation hazard assessment: Predictions from dynamic model. *The American Naturalist*, 139, 161-176.
- Cade, B. S. & Terrell, J. W. 1997. Comment: Cautions on forcing regression equations through the origin. *North American Journal of Fisheries Management*, 17, 225-227.
- Cardenas, Y. L., Shen, B., Zung, L. & Blumstein D. T. 2005. Evaluating temporal and spatial margins of safety in galahs. *Animal Behaviour*, 70, 1395-1399.
- Caro, T. M. 1986a. Ungulate antipredator behaviour: preliminary and comparative data from African bovids. *Behaviour*, 128, 189-228.
- Caro, T. M. 1986b. The functions of stotting in Thomson's gazelles: some tests of the predictions. *Animal Behaviour*, 34, 663-84.
- Caro, T. M., Lombardo, L., Goldizen, A. W. & Kelly, M. 1995. Tail-flagging and other antipredator signals in white tailed deer: New data and synthesis. *Behavioral Ecology*, 6, 442-50.
- Caro, T. M., Graham, C. M., Stoner, C. J. & Vargas, J. K. 2004. Adaptive significance of antipredator behaviour in artiodactyls. *Animal Behaviour*, 67, 205-228.
- Cooper, W. E. 1997. Factors affecting risk and cost of escape by the broad-headed skink (*Emecea laticeps*): predator speed, directness of approach, and female presence. *Herpetologica*, 53, 464-474.

- Cooper, W. E. 2003. Risk factors affecting escape behavior by the desert iguana, *Dipsosaurus dorsalis*: speed and the directness of predator approach, degree of cover, direction of turning by a predator, and temperature. *Canadian Journal of Zoology*, 81, 979-984.
- Cooper, W. E., Perez-Mellado, V., Baird, T., Baird, T. A., Caldwell, J. P. & Vitt L. 2003. Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards, *Cnemidophorus murinus*. *Behavioral Ecology*, 14, 288-293.
- Cooper, W. E., Pérez-Mellado, V. & Hawlena, D. 2006. Magnitude of food reward affects escape behaviour and acceptable risk in Balearic lizards, *Podarcis lilfordi*. *Behavioral Ecology*, 17, 554-559.
- Diego-Rasilla, F. J. 2003. Influence of predation pressure on the escape behaviour of *Podarcis muralis* lizards. *Behavioural Processes*, 63, 1-7.
- Dill, L. M. 1990. Distance-to-cover and the escape decisions of an African cichlid fish, *Melanochromis chipokae*. *Environmental Biology of Fishes*, 27, 147-152.
- Dill, L. M. & Houtman, R. 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus-carolinensis*). *Canadian Journal of Zoology*, 67, 233-235.
- Fernández-Juricic, E. & Schröder, N. 2003. Do variations in scanning behaviour affect tolerance to human disturbance? *Applied Animal Behaviour Science*, 84, 219-234.
- FitzGibbon, C. D. & Fanshawe, J. H. 1988. Stotting in Thomson's gazelle: an honest signal of condition. *Behavioural Ecology and Sociobiology*, 23, 69-74.
- Frid, A. & Dill, L. M. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6, 11. [online] URL: <http://www.consecol.org/vol6/iss1/art11/>
- Holmern, T., Mkama, S. Y., Muya, J. & Røskaft, E. 2006. Intraspecific prey choice of bushmeat hunters outside the Serengeti National Park, Tanzania: a preliminary analysis. *African Zoology*, 41, 81-87.

- Hurley, A. C. & Hartline, P. H. 1974. Escape response in the damselfish *Chromis cyanea* (Pisces: Pomacentridae): a quantitative study. *Animal Behaviour*, 22, 430-437.
- Martín, J. & López, P. 1996. The escape response of juvenile *Psammodromus algirus* lizards. *Journal of Comparative Psychology*, 110, 187-192.
- Neter, J., Kutner, M. H., Nachtsheim, C. J. & Wasserman, W. 1996. Applied linear statistical models, 4th ed. Boston: McGraw Hill.
- R Development Core Team 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Runyan, A. M. & Blumstein, D. T. 2004. Do individual differences influence flight initiation distance? *Journal of Wildlife Management*, 68, 1124-1129.
- Setsaas, T. H. 2004. How Does Human Exploitation Affect Impala (*Aepyceros melampus*) Populations in Protected and Partially Protected Areas? - A Case Study from the Serengeti Ecosystem, Tanzania. M.Sc. thesis. Norwegian University of Science and Technology, Trondheim, Norway.
- SPSS, 2005. SPSS for Windows. Release 14.0. Chicago, IL: SPSS Inc.
- Stankowich, T. & Coss, R. G. 2005. Effects of predator behaviour and proximity on risk assessment by Columbian black-tailed deer. *Behavioural Ecology*, 17, 246-254.
- Stankowich, T. & Blumstein, D. T. 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society of London B*, 272, 2627-2634.
- Stone, P. A., Snell, H. L. & Snell, H. M. 1994. Behavioral diversity as biological diversity: introduced cats and lava lizards wariness. *Conservation Biology*, 8, 569-573.
- Walther, F. R. 1969. Flight behaviour and avoidance of predation in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour*, 34, 185-221.

Ydenberg, R. C. & Dill, L. M. 1986. The economics of fleeing from predators. *Advances in the Study of Behaviour*, 16, 229-49.

Tables:

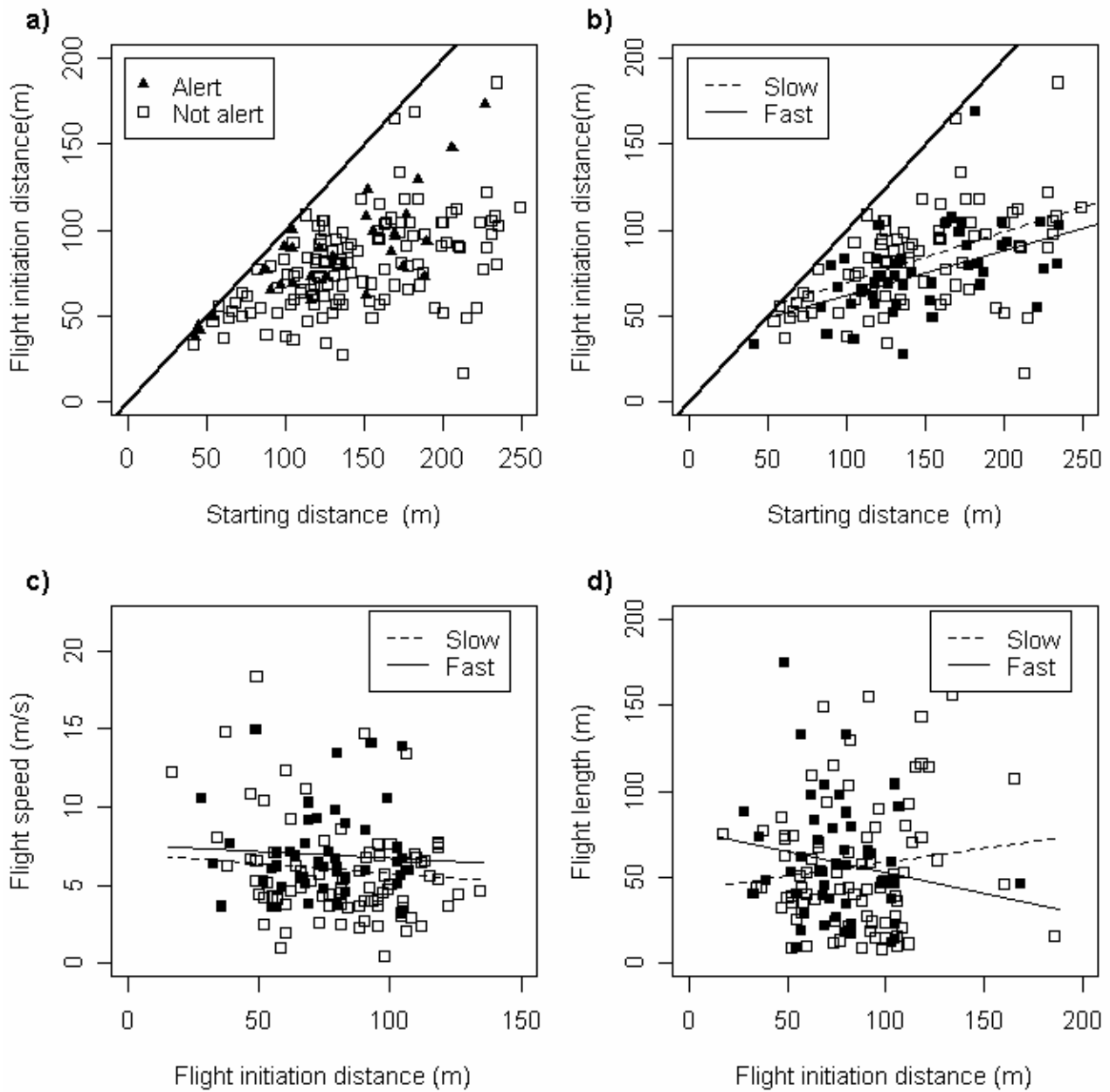
Table 1. Correlation matrix between flight response variables in Thomson's gazelle that displayed not alert behaviour prior to the experimental approach. Within each cell the value of the correlation coefficient r_p and the level of statistical significance P are reported ($n = 129$ for all correlations).

	FID	Starting distance	Flight speed
Starting distance	0.594 <0.001		
Flight speed	0.015 0.859	0.074 0.39	
Flight length	0.087 0.311	0.086 0.312	0.476 <0.001

Figures.

Figure 1. The relationship of approach speed and different flight responses in Thomson's gazelle. The thick line in figure a) and b) represents the 1:1 relationship between the starting distance and FID. Figure a) shows the effect of gazelles displaying alert and not alert behaviour when the trial commenced, whereas figures b) - d) are only on not alert animals. Figure b) shows the effect of approach speed on FID (slow approach: dotted line (□), fast approach: thin line (■)). Figure c) represents the effect of approach speed on flight speed. Lastly, figure d) represents the influence of approach speed on flight length.

Figure 1.



Paper V

Uneconomical game cropping in a community-based conservation project outside the Serengeti National Park, Tanzania

Tomas Holmern, Eivin Røskaft, Job Mbaruka, Samson Y. Mkama and John Muya

Abstract Since 1993 the Serengeti Regional Conservation Project (SRCP) in Tanzania has conducted a game cropping operation (the commercial utilization of wild animal populations in natural habitats) in areas immediately outside the Serengeti National Park in order to provide adjacent villages with incentives to abstain from illegal hunting. In this study we carry out a comparative economic analysis of the SRCP cropping operation and illegal hunting. The extent of illegal hunting was mapped by utilising questionnaires distributed to Village Game Scouts employed in five of the Project villages. Our research indicates that the cropping operation is not economically sustainable and makes only a minor economic contribution to the Project villages compared to

illegal hunting. Furthermore, cropping quotas are small, utilization of quotas low, and the level of community involvement limited. Illegal hunting was extensive around both Project and other villages. We suggest that SRCP discard the inefficient cropping operation and instead concentrate on diversifying income opportunities for the Project villages.

Keywords Community-based conservation, game cropping, hunting, Serengeti, Tanzania.

This paper contains supplementary material that can only be found online at <http://journals.cambridge.org>

Introduction

Community-based conservation (CBC) is now a well established approach to biodiversity conservation throughout Africa (Kiss, 1990; Hulme & Murphree, 2001), although the success of CBC in achieving effective results is being debated (Hackel, 1999; Songorwa *et al.*, 2000; Newmark & Hough, 2000; Adams & Hulme, 2001). Conservation benefits to communities from CBC in eastern and southern Africa are generally acquired through the retention of revenues from the tourist industry and/or different types of wildlife utilization schemes (Child, 1996; Lewis & Alpert, 1997; Bergin, 2001).

Several of the CBC projects in Tanzania emphasize the sustainable use of surrounding wildlife resources (Walsh 1998; Songorwa, 1999). Immediately outside the Serengeti National Park, the Serengeti Regional Conservation Project (SRCP) has run a game cropping (the commercial utilization of wild animal populations in natural habitats) operation since 1993 in the adjacent Grumeti and Ikorongo Game Reserves and neighbour-

ing Ikona Wildlife Management Area to provide communities with incentives to abstain from illegal hunting (Mbano *et al.*, 1995). The Norwegian Agency for Development Cooperation and the Tanzanian government has supported SRCP since 1987, and in the period 1998–2002 US \$330,000 has been provided annually (Havnevik *et al.*, 2001).

Illegal hunting is considered a serious threat to the Serengeti ecosystem and has reduced the populations of buffalo *Syncerus caffer* by 50–90% in parts of their range (Dublin *et al.*, 1990). Other resident wildlife, such as giraffe *Giraffa camelopardis*, impala *Aepyceros melampus* and topi *Damiliscus korrigum* are also experiencing heavy hunting pressure in areas close to the protected area boundaries (Campbell & Borner, 1995; Hofer *et al.*, 1996). The main hunting method in the Serengeti is the use of snares, but night hunting with torches and hunting dogs has also become common (Arcese *et al.*, 1995; Holmern, 2000). Illegal hunting is highly profitable over large tracts of the protected area (Hofer *et al.*, 2000).

In this study we use the SRCP and other areas outside the Serengeti National Park as a case study. We conduct a comparative economic analysis of the SRCP cropping operation and illegal hunting, in order to assess the economic sustainability of the two systems.

Study area

The study was conducted in Bunda and Serengeti Districts adjacent to the Western Corridor of the Serengeti National Park (Fig. 1). The study area lies at

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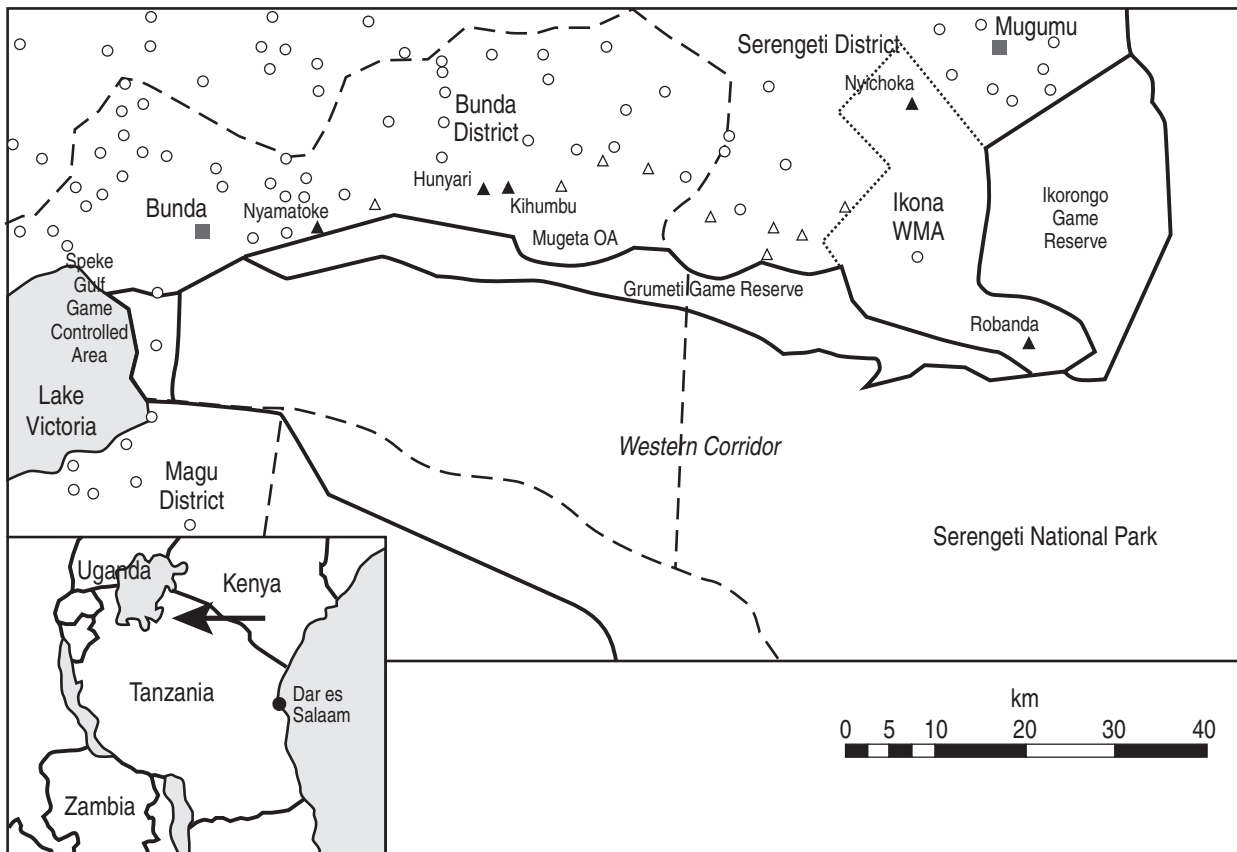


Fig. 1 The Western Corridor of the Serengeti National Park with the approximate locations of villages. Triangles are the 14 project villages and filled triangles indicate the five project villages included in the survey of illegal hunting by Village Game Scouts. Squares are district administrative towns and open circles are all other villages. The dashed line represents district boundaries, thick lines denote the protected areas and the dotted line represents Ikorongo Wildlife Management Area. The arrow on the inset map indicates the location of the main figure.

altitudes of 920–1,500 m, the mean annual temperature is 21.7°C, and the mean annual total precipitation varies from 800 mm in the east to 1,050 mm in the north-west (Campbell & Hofer, 1995). Serengeti District contains relatively intact thorn tree woodlands and plains (with species of *Acacia*, *Comiphora*, *Ficus*, *Combretum* and *Podocarpus*) in Ikorongo Wildlife Management Area (Herlocker, 1976). In Bunda District the areas to the west are largely treeless, and extensive areas adjacent to the Grumeti Game Reserve and Serengeti National Park have been converted to agriculture.

The Western Corridor of the Serengeti National Park is characterized by the annual migration of wildebeest *Connochaetes taurinus* (McNaughton & Banyikwa, 1995). Normally the migratory herds reach this area in May or June. The duration of their stay depends on rainfall, but usually the herds have moved to their dry season areas in the northern Serengeti and Masai Mara National Reserve by August (Maddock, 1979).

Bunda and Serengeti Districts had human populations of 200,870 and 113,284, respectively, in the last National

Census in 1988, and an average annual population increase of 3.1% (Bureau of Statistics, 1988). Tanzania is poor economically and in 2000 had a gross per capita income of US \$270 (World Bank, 2000). Most of the multi-ethnic communities in the study area practice subsistence farming, complemented to varying degrees by livestock keeping and illegal hunting (Mtoni, 1999).

Materials and methods

The SRCP cropping operation

The cropping operation, which began in 1993, includes 14 villages in Bunda and Serengeti Districts (Fig. 1). The aim of the cropping operation is to provide communities with legal meat and to 'play a central role in the economic development of the project's villages' (SRCS, 1995). The species cropped (wildebeest, zebra *Equus burchelli*, and topi) were chosen on the basis of their potential meat yield and skin value. Topi was first added to the quota in 1995 (Table 1). SRCP is allocated a quota

Table 1 The quota, number cropped and percentage of the quota utilized for the three species (wildebeest, zebra and topi), in the game cropping scheme from 1993 to 1999.

Year	Wildebeest			Zebra			Topi ^c		
	Quota	Cropped	%	Quota	Cropped	%	Quota	Cropped	%
1993	480	94	19.6	192	63	32.8			
1994	700	108	15.4	90	25	27.8			
1995	592	227	38.3	64	29	45.3	39	22	56.4
1996	500	117	23.4	70	70	100	50	50	100
1997 ^a	250	–	–	140	–	–	100	–	–
1998	300	108	36.0	180	60	33.3	100	42	42.0
1999 ^b	210	–	–	140	–	–	70	–	–

^aData for number cropped were not available for 1997.

^bRecords of the number of animals cropped was only available up to November 1998.

^cTopi was only added to the quota from 1995 onwards.

directly by the Wildlife Department and it is divided equally among the Project villages. The cropping team are required to follow the normal hunting season (1 July–31 December), but can hunt outside the season with permission from the Wildlife Department.

The cropping takes place mainly in Grumeti Game Reserve (*c.* 416 km²) and Ikona Wildlife Management Area (*c.* 600 km²) (Fig. 1), and occasionally in Ikorongo Game Reserve (*c.* 563 km²). Animals are shot during the day from a four-wheel drive vehicle and, because the meat is consumed locally, it is not subject to any health rules. The Natural Resource Committee in each of the Project villages organizes the sale and determines the price of the fresh meat (in the range US \$0.27–0.40 per kg). The skins are processed by local skinners. All expenses associated with the cropping operation are covered by SRCP, and all income is retained in the Project villages. The income has been used for reducing the tax burden in Project villages, in addition to building classrooms, dispensaries, and houses for nurses and teachers.

Survey of illegal hunting

To document patrol efforts and illegal hunting Village Game Scouts (VGS) in five Project villages (Fig. 1) filled out questionnaires during patrols from December 1998 to August 1999. The five participating Project villages were chosen because they had functioning VGS teams and were evenly distributed within the study area. The questionnaire (Appendix 1), written in KiSwahili, contained 20 questions on the patrol, arrested hunter(s), methods of hunting, and the species recovered. No differentiation was made between porters and hunters. We provided the VGS with training in how to fill out the questionnaire, and held follow-up meetings with them, with the help of a local interpreter, two times per village per month for the first 3 months and the last

2 months of the survey. During these follow-up meetings T.H. collected the questionnaires and all hunting equipment seized by the VGS. In the period when T.H. was absent hunting questionnaires and equipment was delivered to the local game post or Ikorongo Grumeti Game Reserve headquarters. In 17% of the 201 patrols during the survey period District Game Scouts accompanied the VGS.

Information from the questionnaires, together with household data for the Project villages from the most recent, 1993, census for the area (Kauzeni & Kiwasila, 1994), was used to quantify the economic value of illegal hunting. To determine the number of illegal hunters originating from all 14 Project villages combined we calculated the proportion of the local residents engaged in hunting in protected areas, as a function of the distance of the home village from the boundary of the nearest protected area border (Appendix 2). Distances were determined using the 1:50,000 topographic maps of the Surveys and Mapping Division, Ministry of Lands, Houses and Urban Development. By multiplying, for each village, the proportion of local residents engaged in hunting by the village population size, we derived an estimate of the total number of hunters in the 14 Project villages.

Through discussions with a total of 41 VGS and district game scouts we determined the price of dried and fresh meat in the Project villages that was derived from illegal hunting (the game meat of species with body sizes greater than impala is usually sold or bartered as dried meat, whereas that of smaller species is usually sold as fresh meat). Using this information we determined the mean annual economic value of game meat to a hunter (Appendix 2), and multiplied this by the estimate of the total number of hunters to obtain an estimate of the total economic value of illegal hunting to the 14 Project villages. When estimating the economic

Table 2 The number and total dressed carcass weight in kg of wildebeest, zebra and topi allocated to the 14 Project villages from the July 1999 game cropping trip with, for each village, its population size, distance from the nearest protected area, number of households, proportion of residents per household hunting (see text and Appendix 2 for details), and estimated number of hunters.

Village	Wildebeest		Zebra		Topi		Population size (1993 census)	Distance from nearest protected area (km) ^a	No. of households	Proportion of residents hunting (y) ^b	No. of hunters (= y *population size)
	no.	kg	no.	kg	no.	kg					
Robanda	2	154	–	–	–	–	1,582	4	150	0.119	188.3
Nyichoka	2	141	–	–	–	–	1,956	8	365	0.068	133.0
Nyakitono	2	150	–	–	–	–	1,065	8	184	0.068	72.4
Natta-Mbiso	3	175	1	75	–	–	2,119	5	294	0.104	220.4
Motukeri	2	139	1	128	–	–	3,316	6	257	0.090	298.4
Singisi	1	53	–	–	2	112	1,525	1.5	176	0.147 ^c	224.2
Iharara	–	–	–	–	2	127	1,810	6.5	192	0.084	152.0
Kyandege	–	–	–	–	3	158	5,600	9.5	778	0.056	313.6
Mugeta	2	146	–	–	1	74	3,300	12	458	0.039	128.7
Mariwanda	4	202	–	–	2	101	3,274	6.5	408	0.084	275.0
Kihumbu	4	247	–	–	1	53	1,850	5.5	200	0.097	179.5
Hunyari	4	233	1	101	1	34	4,800	6	364	0.090	432.0
Mihale	2	180	–	–	–	–	2,280	2	335	0.147 ^c	335.2
Nyamatoke	3	249	–	–	–	–	2,185	2.5	321	0.147	321.2
Total	31	2,069	3	304	12	659	36,662		4,482		3,273.9

^aMeasured from the centre point of the project village to the boundary of the closest protected area.

^bCalculated using equation 1 in Appendix 2.

^cWhen calculating y for villages <2.5 km from the nearest protected area, distance was set to 2.5 km (see Appendix 2 for details).

value we disregarded the value of the animal skins. Because they are evidence of illegal hunting they are usually discarded before hunters return to the villages (J. Wilton, pers. comm.).

SPSS 8.0 (SPSS, Inc., Chicago, USA) was used for all statistical analyses.

Results

The economics of the cropping operation

Due to the limited record keeping by SRCP we obtained complete records for only one cropping trip, for July 1999 (Table 2). Cropping trips are budgeted to take a fortnight and usually consist of two game scouts and a Project officer, but consisted on this occasion of three game scouts because a Project officer was not available. The Project villages normally cover half of the ammunition cost, but in the calculations presented here (Table 3) this is incorporated into the total ammunition cost.

On this trip a total of 46 animals were shot (Table 2), and on average the marksman used 4.3 rounds of ammunition per animal. Data was not available on the number of animals wounded and not recovered as carcasses, or on the sex and age of the cropped animals. With an estimated income of US \$1,016 and total expenses of US \$1,673, this cropping trip had a deficit of US \$657 (Table 3). Income from the sale of skins was

Table 3 Total income, total expenses and balance (US \$) from the July 1999 game cropping trip (see Table 2).

Item	Details ^c	US \$
Total income ^a	\$0.335 per kg* 3,032 kg	1,015.7
Expenses		
Staff Salaries	\$1.72 per day* 3 GS* 15 days	77.4
Staff Allowances	8 days* 3 GS* \$11.33	271.9
	6 days* 3 GS* \$8.67	156.1
Fuel	280 litres* \$0.67	187.6
Emergency fund		40.0
Ammunition	56 rounds (0.303) at \$1.33 per round	74.5
	140 rounds (0.220) at \$0.67 per round	93.8
Vehicle maintenance cost ^b	\$0.54 per km* 1,429 km	771.7
Total expenses		–1,672.9
Balance		–657.2

^aThere is no monitoring of income from the sale of meat in the villages, and therefore the figures are estimated on the basis of the total weight of meat given to each village.

^bTaken from Hough (1993) and adjusted for inflation.

^cGS = game scout.

not incorporated as few skins are sold due to marketing difficulties and poor quality. If the annual quota for 1999 (Table 1) had been fully utilized it would have yielded a total value of US \$10,735 at US \$0.335 per kg but, using the mean annual utilization of 43.9%, the value realized for 1999 would have been only US \$4,713.

Estimated economic value of illegal hunting

The VGS conducted 201 patrols from December 1998 to August 1999, both during the day and night, with a mean of $20.8 \pm \text{SE } 0.3$ patrols per month, and arrested an average of $0.5 \pm \text{SE } 0.1$ illegal hunters per patrol. A total of 634 snares (a mean of $3.1 \pm \text{SE } 0.4$ snares per patrol) were collected. Thirty-two pitfall traps were recorded, but no firearms were reported. The VGS observed a total of 111 hunting groups, with a mean of $3.8 \pm \text{SE } 0.6$ hunters per group. During these patrols a total of 96 hunters from 13 tribes, all male, were apprehended for hunting without a licence, and 80 of these answered questions put to them (Appendix 1) about their illegal hunting. The arrested hunters originated from 23 different villages in the Mara Region, both Project and other villages. The mean straight line distance from an 'arrest site' (the centre point of the location name recorded by the VGS) to hunters' home villages was $13.9 \pm \text{SE } 1.6$ km, maximum 60.5 km ($n = 76$). Of the hunters who replied to the reason for hunting ($n = 71$), 60.5% stated that they hunted for their own consumption, 8.5% that they hunted only for profit, and 31% that

they hunted for both purposes. A total of 88 animals of eight species were found with the arrested hunters (81% migratory animals and 19% resident) (Table 4).

The hunters spent $3.9 \pm \text{SE } 0.5$ days ($n = 62$) out hunting before being caught, and the stated length of an average hunting trip was $6.8 \pm \text{SE } 0.8$ days ($n = 52$). The mean number of annual trips per hunter was $12.9 \pm \text{SE } 1.8$ (range 1–44, $n = 41$). On average a hunter killed $0.92 \pm \text{SE } 0.1$ animal per trip. The average annual wildlife harvest per hunter was therefore found to be 11.9 animals per year: 9.6 migratory and 2.3 resident. The hunters went on significantly more hunting trips during the dry season than the wet season (Mann Whitney, $Z = -2.358$, $P = 0.018$).

Using the commercial prices of meat from animals hunted illegally (Table 5) the mean annual economic value of the wildlife harvest per hunter (E , Appendix 2) was calculated to be US \$64.8 \pm 95% CI 18.5. We estimated that a total of 3,274 hunters (Table 2), who harvested 38,960 animals, originated from the 14 Project villages. Using this and the estimated mean annual economic value of game meat to a hunter gives an estimated total economic value for the illegal wildlife harvest of

Table 4 Numbers of each of the eight species recovered from 96 illegal hunters, categorized according to the reasons given by the hunters for hunting each species, and the migratory or resident status of each species.

Species	Status	Reason given for hunting				Total
		Own consumption	Market	Both	Unknown	
Wildebeest <i>Connochaetes taurinus</i>	migratory	20	1	7	11	39
Thomson's gazelle <i>Gazella thomsoni</i>	migratory	25	2	–	2	29
Impala <i>Aepyceros melampus</i>	resident	5	–	5	1	11
Zebra <i>Equus burchelli</i>	migratory	1	–	2	–	3
Warthog <i>Phacochoerus aethiopicus</i>	resident	–	–	3	–	3
Topi <i>Damalisca korrigum</i>	resident	–	–	1	–	1
Reedbuck <i>Redunca redunca</i>	resident	1	–	–	–	1
Gray duiker <i>Sylvicapra grimmia</i>	resident	1	–	–	–	1
Total		53	3	18	14	88

Table 5 Commercial price (US \$, see text for details) of the meat of the eight species hunted illegally.

Species	No. of pieces per carcass	Total value of carcass \pm SE	
		Wet season	Dry season
Prices for dried meat			
Zebra <i>Equus burchelli</i>	15	21.5 \pm 3.0	12.3 \pm 1.5
Wildebeest <i>Connochaetes taurinus</i>	11	10.3 \pm 1.8	5.7 \pm 1.0
Topi <i>Damalisca korrigum</i>	11	10.3 \pm 1.8	6.0 \pm 1.0
Prices for fresh meat			
Impala <i>Aepyceros melampus</i>	6	8.3 \pm 1.3	5.4 \pm 1.1
Warthog <i>Phacochoerus aethiopicus</i>	6	8.6 \pm 1.2	5.6 \pm 1.0
Reedbuck <i>Redunca redunca</i>	6	8.3 \pm 1.3	5.4 \pm 1.1
Thomson's gazelle <i>Gazella thomsoni</i>	4	4.4 \pm 0.6	2.7 \pm 0.6
Gray duiker <i>Sylvicapra grimmia</i>	4	4.4 \pm 0.6	2.7 \pm 0.6

US \$212,155 \pm 95% CI 60,569. Using a conservative estimate of one adult male per household, illegal hunters constitute 73% of the adult male population of the Project villages (Table 2).

Discussion

Game cropping has been proposed and used as a means of giving rural communities economic benefits from living next to protected areas in Africa (Myers, 1981; Mbanjo *et al.*, 1995), although caution has been urged in exercising this approach (Parker, 1984; Macnab, 1991; Barrett & Arcese, 1995). The SRCP cropping operation has been running for several years, but the percentage of the quota utilized has generally been low (Table 1). Both Ikorongo and Grumeti Game Reserves and surrounding non-protected areas, where the cropping takes place, are over-exploited and contain little resident wildlife (Cambell & Borner, 1995). Cropping is therefore largely dependent on migratory herds, which only spend brief periods in the cropping area. These facts, together with logistical problems such as the use of only one vehicle, the long distances involved and poor infrastructure, explain why the utilization of the quota remains low. In addition, the quota for each of the 14 Project villages is small, which limits the cropping scheme's impact on individual villages. As illegal hunting generates an economic value 45 times greater than that derived from the cropping operation, the latter is therefore, in itself, unlikely to put an end to illegal hunting.

The running cost of the July 1999 cropping operation exceeded the revenue that it generated, but it could be argued that this single trip is not representative of the whole cropping season. However, we believe that the deficit from the trip is probably an underestimate of the general deficit because: (1) game cropping undertaken after migratory animals move out of the area will yield fewer animals, (2) the distance travelled during each cropping trip will increase after the migratory herds move on because animals become harder to locate and more wary, and (3) planning costs, the inclusion of a Project officer during cropping, and the purchase of the vehicle and firearms are not included in the cost estimate. Although the cropping operation runs at a deficit, SRCP covers all costs and therefore cropping still remains lucrative to the Project villages who retain all income generated from the sale of meat.

A large number of bullets were used per animal on the July 1999 cropping trip (4.3 rounds). This low efficiency may be due to: (1) unreported carcasses, (2) poor marksmanship, (3) difficult cropping conditions (large flight distance, difficult terrain and daylight cropping), and (4) the absence of a Project officer on the trip. By

comparison Mphande & Jamusana (1984) stated that the culling of nyala antelopes *Tragelaphus angasi* in Malawi, conducted at night with the use of a spotlight, used on average only 1.03 rounds per animal.

Although fresh meat from the cropping operation is cheaper (US \$0.27–0.40 per kg) than locally bought beef (US \$1.1 per kg), the poorer households may still not have cash, and it is therefore the relatively affluent households that are able to more readily take advantage of the availability of legal fresh game meat. The utilization of wildlife resources by local communities is often both for household consumption and income (Marks, 1973; Campbell & Hofer, 1995; Carpaneto & Fusari, 2000). The majority of the illegal hunters arrested during the patrols stated they were hunting for their own consumption. Wildlife food sources are important locally because several of the villages in the study area do not have a sufficient supply of food crops to survive only on agriculture (Iwai, 1997; Mtoni, 1999). However, the data collected needs to be treated cautiously, as the hunters may have been afraid of replying that they hunted for income, and subsistence hunters who hunt illegally to supply their family with meat may also switch to commercial hunting (for sale or barter), depending on the demand for game meat and the degree of poverty in their household (Hofer *et al.*, 1996; Barrett & Arcese, 1998).

Our method of collecting information on illegal hunting could have introduced biases in the calculations of our estimates. Because the dry season months of September–November were not included we may have underestimated the mean economic value of game meat to each hunter. Furthermore, arrested hunters may have under-reported the number of animals killed during hunting trips and the number of hunting trips in each season, because of fear of punishment (although arrested hunters were not punished according to their level of hunting). Although Rugumayo (1996) reported that illegal hunting from the Project villages is on the decline, which could weaken the model of Campbell & Hofer (1995) the proportion of local residents per household engaged in hunting (Appendix 2), the level of hunting activity around the Project villages suggests that the model is still valid.

In recent years SRCP, together with the community conservation programme of Tanzania National Parks, has worked extensively with local communities around the Serengeti National Park to raise awareness about hunting issues and to encourage the establishment of small-scale economic projects. SRCP has also helped some of the Project villages organise wildlife management areas, which may generate income in the future, and trophy hunting and photo safaris could provide a further source of income. Such initiatives may not,

however, necessarily provide sufficient incentives for the cessation of illegal hunting, as it also has cultural and recreational motives that remain unaddressed (Gibson & Marks, 1995; Lewis & Phiri, 1998; Infield, 2001).

To be able to improve the long-term conservation of the Serengeti ecosystem, managers need to address the cause and not the symptoms of illegal hunting. Widespread poverty provides the incentive for illegal hunting, and hunting will continue as long as alternative sources of income are unavailable. The SRCP game cropping has small quotas for each Project village, generates little revenue, and involves Project villages to only a limited degree. It will not be able to sustain itself beyond donor support. We therefore recommend that SRCP discards the game cropping operation in favour of a diversification of income opportunities for the Project villages in areas such as agriculture and tourism. In this context SRCP needs to continue its cooperation with organizations that have adequate expertise in extension services.

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References

- Adam, W.M. & Hulme, D. (2001). If community conservation is the answer, what is the question? *Oryx*, **35**, 193–201.
- Arcese, P., Hando, J. & Campbell, K. (1995) Historical and present day anti-poaching efforts in Serengeti. In *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 506–533. University of Chicago Press, Chicago, USA.
- Barrett, C.B. & Arcese, P. (1995) Are integrated conservation-development projects (ICDPS) sustainable? On the Conservation of large mammals in sub-Saharan Africa. *World Development*, **23**, 1073–1084.
- Barrett, C.B. & Arcese, P. (1998) Wildlife harvest in integrated conservation and development projects: linking harvest to household demand, agricultural production, and environmental shocks in the Serengeti. *Land Economics*, **74**, 449–65.
- Bergin, P. (2001) Accommodating new narratives in a conservation bureaucracy: TANAPA & community conservation. In *African Wildlife and Livelihoods: The Promise and Performance of Community Conservation* (eds D. Hulme & M. Murphree), pp. 88–105. James Curry, Oxford and Heinemann, New Hampshire.
- Bureau of Statistics (1988) *Population Census: Preliminary Report*. Ministry of Finance, Economic Affairs and Planning, Dar es Salaam, Tanzania.
- Campbell, K.L.I. & Borner, M. (1995) Population trends and distribution of Serengeti herbivores: implications for management. In *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 117–145. University of Chicago Press, Chicago, USA.
- Campbell, K.L.I. & Hofer, H. (1995) People and wildlife: spatial dynamics and zones of interaction. In *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 534–570. University of Chicago Press, Chicago, USA.
- Carpaneto, G.M. & Fusari, A. (2000) Subsistence hunting and bushmeat exploitation in central-western Tanzania. *Biodiversity and Conservation*, **9**, 1571–1585.
- Child, G. (1996) The role of community-based wild resource management in Zimbabwe. *Biodiversity and Conservation*, **5**, 355–367.
- Dublin, H.T., Sinclair, A.R.E., Boutin, S., Anderson, E., Jago, M. & Arcese, P. (1990) Does competition regulate ungulate populations? Further evidence from Serengeti, Tanzania. *Oecologia*, **82**, 283–288.
- Gibson, C.C. & Marks, S.A. (1995) Transforming rural hunters into conservationists- an assessment of community-based wildlife management programs in Africa. *World Development*, **23**, 941–957.
- Hackel, J.D. (1999) Community Conservation and the future of Africa's wildlife. *Conservation Biology*, **13**, 726–734.
- Havnevik, K.J., Monela, G., Jingu, R., Rugumayo, C.R. & Røskaft, E. (2001) *Management of Natural Resources Programme, Tanzania, Phase II (1998–2002). Mid-term Review*. Report presented to the Royal Norwegian Embassy, Dar es Salaam and the Ministry of Natural Resources and Tourism, Tanzania.
- Herlocker, D. (1976) *Woody Vegetation of the Serengeti National Park*. Texas A & M University, College Station, USA.
- Hofer, H., Campbell, K.L.I., East, M.L. & Huish, S.A. (1996) The impact of game meat hunting on target and non-target species in the Serengeti. In *The Exploitation of Mammal Populations* (eds J. Taylor & N. Dunstone), pp. 117–146. Chapman and Hall, London, UK.
- Hofer, H., Campbell, K.L.I., East, M.L. & Huish, S.A. (2000) Modeling the spatial distribution of the economic costs and benefits of illegal game meat hunting in the Serengeti. *Natural Resource Modeling*, **13**, 151–177.
- Holmern, T. (2000) *Hunting and community-based conservation outside the Serengeti National Park – A sustainable approach by Serengeti Regional Conservation Project (SRCP)?* MSc thesis, Norwegian University for Science and Technology, Trondheim, Norway.

- Hough, J.L. (1993) *Community Hunting Experiments*. Unpublished technical report. Report no. 2, Serengeti Regional Conservation Strategy, Tanzania.
- Hulme, D. & Murphree, M. (eds) (2001) *African Wildlife and Livelihoods – The Promise and Performance of Community Conservation*. James Curry, Oxford and Heinemann, New Hampshire, USA.
- Infield, M. (2001) Cultural values: a forgotten strategy for building community support for protected areas in Africa. *Conservation Biology*, **15**, 800–802.
- Iwai, Y. (1997) *Subsistence strategies of households in Robanda Village adjacent to Serengeti National Park, Tanzania*. MA thesis, Kyoto University, Kyoto, Japan.
- Kauzeni, A.S. & Kiwasila, H.L. (1994) *Serengeti Regional Conservation Strategy: a Socioeconomic Study*. Institute of Resource Assessment, University of Dar es Salaam, Dar es Salaam, Tanzania.
- Kiss, A. (ed.) (1990) *Living with Wildlife: Wildlife Resource Management with Local Participation in Africa*. Technical Paper Number 130, World Bank, Washington, DC, USA.
- Lewis, D.M. & Alpert, P. (1997) Trophy hunting and wildlife conservation in Zambia. *Conservation Biology*, **11**, 59–68.
- Lewis, D.M., Kaweche, G.B. & Mwenya, A. (1990) Wildlife conservation outside protected areas – lessons from an experiment in Zambia. *Conservation Biology*, **4**, 171–180.
- Lewis, D.M. & Phiri, A. (1998) Wildlife snaring – an indicator of community response to a community-based conservation project. *Oryx*, **32**, 111–121.
- Maddock, L. (1979) The 'migration' and grazing succession. In *Serengeti, Dynamics of an Ecosystem* (eds A.R.E. Sinclair & M. Norton-Griffiths), pp. 104–129. University of Chicago Press, Chicago, USA.
- Marks, S.A. (1973) Prey selection and annual harvest of game in a rural Zambian community. *East African Wildlife Journal*, **11**, 113–128.
- Mbano, B.N.N., Malpas, R.C., Maige, M.K.S., Symonds, P.A.K. & Thompson, D.M. (1995) The Serengeti Regional Conservation Strategy. In *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 605–616. University of Chicago Press, Chicago, USA.
- Macnab, J. (1991) Does game cropping serve conservation? A re-examination of the African data. *Canadian Journal of Zoology*, **69**, 2203–2290.
- McNaughton, S.J. & Banyikwa, F. (1995) Plant communities and herbivory. In *Serengeti II – Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 49–70. University of Chicago Press, Chicago, USA.
- Mphande, J.N.B. & Jamusana, H.S. (1984) Culling of nyala antelopes in Lengwe National Park, Malawi. In *Conservation and wildlife resources in Africa* (eds R.H.V. Bell & E. McShane-Caluzi), pp. 256–277. Peace Corps, Washington, DC, USA.
- Mtoni, P.E. (1999) *Involve them or lose them both: local communities surrounding Serengeti National Park in Bunda and Serengeti Districts in relation to wildlife conservation*. MSc thesis, Agricultural University of Norway, Ås, Norway.
- Myers, N. (1981) The canning of Africa. *Science Digest*, **8**, 72–119.
- Newmark, W.D. & Hough, J.L. (2000) Conserving wildlife in Africa: integrated conservation and development projects and beyond. *Bioscience*, **50**, 585–592.
- Parker, I.S.C. (1984) Perspectives on wildlife cropping or culling. In *Conservation and Wildlife Resources in Africa* (eds R.H.V. Bell & E. McShane-Caluzi), pp. 233–253. Peace Corps, Washington, DC, USA.
- Rugumayo, C.R. (1996) *Participation in Sustainable Resource Utilisation and Benefit Sharing. The Case of Serengeti Regional Conservation Strategy, Tanzania*. NIBR Working Paper, Oslo, Norway.
- Songorwa, A.N. (1999) Community-based wildlife management (CWM) in Tanzania: are the communities interested? *World Development*, **27**, 2061–2079.
- Songorwa, A.N., Buhrs, T. & Hughey, K.F.D. (2000) Community-based wildlife management in Africa: a critical assessment of the literature. *Natural Resources Journal*, **40**, 603–643.
- SRCS (Serengeti Regional Conservation Strategy) (1995) *Implementation Report of the Development Activities for the Financial Year 1995/96*. Unpublished report. Ministry of Natural Resources and Tourism (Wildlife Division), Tanzania.
- Walsh, M. (1998) *Notes for Mbomipa Project Visitors*. Unpublished report no. MMN1, August 1998. Ministry of Natural Resources and Tourism (Wildlife Division), Tanzania.
- World Bank (2000) *Data and Statistics: GNI per capita 2000, Atlas method and PPP*. <http://www.worldbank.org/data/datatopic/GNPPC.pdf> [accessed 6 August 2002].

Biographical sketches

Tomas Holmern is interested in natural resource management. He is currently working as a consultant for the Department of Zoology, Norwegian University for Science and Technology.

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Appendix 1

Appendix 1 for this article is available online at <http://journals.cambridge.org>

Appendix 2

The proportion y of the local residents of a village engaged in hunting in the nearest protected area was calculated as:

$$y = 0.208e^{-0.139x} \quad (1)$$

where x is the distance in km from the village to the nearest protected area border (Serengeti National Park, Ikorongo Game Reserve or Grumeti Game Reserve). This function was determined (Campbell & Hofer, 1995) from a best fit curve for 10 villages that lay 2.5–48 km from

a protected area. The function declines exponentially with the distance of the village from the protected area. Because Campbell & Hofer (1995) did not utilize data from villages <2.5 km from a protected area, for the two villages that were closer than this distance (Table 2) x was set at 2.5.

The mean annual economic value of game meat (E) to a hunter was calculated as

$$E = \left\{ \sum_{i=1}^7 \left[\left(\frac{5}{12} S p_i P w_i K \right) + \left(\frac{7}{12} S p_i P d_i K \right) \right] \right\} + \{ S p_w P_w K \} \quad (2)$$

where i are the seven species taken by hunters that are available in both the dry (June–December, i.e. 7 months) and wet (January–May, i.e. 5 months) seasons, $S p_i$ is the proportion that each species contributes to the average wildlife harvest for each hunter as derived from the total number of animals confiscated from arrested hunters (Table 4), $P w_i$ and $P d_i$ are the game meat prices in the wet and dry season respectively, and K is the mean number of animals taken per year per hunter. Wildebeest, w , is only available in the study area in the dry season (Maddock, 1979). We assumed that, except for wildebeest, the availability of all species was the same regardless of season.

Uneconomical game cropping in a community-based conservation project outside the Serengeti National Park, Tanzania

Tomas Holmern, Eivin Røskraft, Job Mbaruka, Samson Y. Mkama and John Muya

Appendix 1

This is an English translation of the questionnaire, originally written in KiSwahili, used by Village Game Scouts in the survey of illegal hunting carried out from December 1998 to August 1999 (see text for details).

Village Game Scout Poaching Survey Number _____
 A. Name _____ B. Village _____
 C. Departure time _____ D. Duration of patrol: hours _____ days _____
 E. No. of game scouts on patrol _____

If a wire snare, pitfall or animal is found, answer questions 1–2 and 19–20.

If poacher(s) only observed, answer questions 1–3.

If poacher(s) apprehended, answer questions 1–20.

1. Date _____
2. Place of capture/finding/observation. _____
3. No. of poachers observed _____
4. No. of poachers arrested _____
5. Name of poacher _____
6. Home village _____
7. Age _____
8. Sex: Male female
9. Tribe _____
10. Household size _____
11. Is the animal hunted for: Own consumption Market Traditional uses Other _____
12. Average monthly income from hunting in Tanzanian shillings _____
13. If the meat is for the market, how much do you get for 1 kg of fresh or dry meat in Tanzanian shillings:
 Wildebeest _____ Zebra _____ Topi _____ Impala _____
14. No. of days spent hunting on this trip _____
15. No. of days spent on an average hunting trip _____
16. How many trips do you make a) During the dry season _____ b) During the wet season _____
17. Total number of hunting trips during a year _____
18. Method of poaching:
 Wire No. _____; Spring trap No. _____; Rope net No. _____; Pit fall No. _____
 Bow No. _____, Arrows No. _____; Dog No. _____; Firearm No. _____
 Type of firearm _____, Bullets Type _____ No. _____; Torch No. _____; Spear No. _____
 Other types of weapon Specify _____, No. _____
19. Animals caught:

Species	Number	Weight (kg)	Sex	Age	Weapon used

20. Give a description of the place of capture or where the snare/pitfall was found: open grassland , open woodland , Dense woodland , Near the river/riverine vegetation , Other, specify _____
 (If there is not enough room please use the other side of the form)

Paper VI

Paper VI is not included due to copyright

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 <i>Pisum sativum</i> and <i>Arabidopsis thaliana</i>
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympatric species of newts (<i>Triturus</i> , <i>Amphibia</i>) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook <i>Corvus frugilegus</i> .
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinizing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed 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 (<i>Trichoptera</i>) 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 <i>Oweniimorpha</i> and <i>Terebellomorpha</i> , 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 <i>Parus montanus</i> .

1987 Jarle Inge Holten	Dr. philos Bothany	Autecological investigations along a coast-inland transect at Nord-Møre, Central Norway
1987 Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of <i>Nicotiana sanderae</i> and <i>Chrysanthemum morifolium</i>
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 (<i>Salmo salar</i>): 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 (<i>Mytilus edulis</i>).
1988 Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (<i>Salmo salar</i> 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 <i>Alces alces</i> .
1989 Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose <i>Alces alces</i> , 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 salmon (<i>Salmo salar</i>) and brown trout (<i>Salmo trutta</i>): 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 <i>Pica pica</i> .
1991 Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (<i>Lynx lynx</i>) in Norway.
1991 Jan Henning L'Abée Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout <i>Salmo trutta</i> and roach <i>Rutilus rutilus</i> 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 <i>Coregonus</i> and <i>Salvelinus</i> : 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 (<i>Phleum pratense</i> L.)
1992 Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins <i>Fratercula arctica</i>
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, <i>Salmo salar</i> L.: Basal and stressor-induced variations in plasma levels and 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 <i>Lutra lutra</i> .
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 (<i>Gallinago media</i>): 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 <i>Phalacrocorax carbo carbo</i> .
1994 Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (<i>Rubus idaeus</i> 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, <i>Vulpes vulpes</i> .
1994 Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cuckoo.
1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss <i>Dicranum majus</i> 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 <i>Lutra lutra</i> distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink <i>Mustela vison</i> .
1995 Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel <i>Thalassoica antarctica</i> ; 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 <i>Mysis relicta</i> and constraints on Cladoceran and Char populations.
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the <i>Schistidium apocarpum</i> complex in Norway and Sweden.
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; impact fish-bacterial interactions on growth and survival of larvae.
1996 Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjörg Einarisdottir	Dr. scient. Zoology	Production of Atlantic salmon (<i>Salmo salar</i>) and Arctic charr (<i>Salvelinus alpinus</i>): 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 <i>Mytilus edulis</i> and the effects of organic xenobiotics.
1996 Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal <i>Halichoerus grypus</i> and Harbour seal <i>Phoca vitulina</i> in the Barents sea region.
1997 Gunvor Øie	Dr. scient Bothany	Eevaluation of rotifer <i>Brachionus plicatilis</i> quality in early first feeding of turbot <i>Scophthalmus maximus</i> L. larvae.
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spruce 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 <i>Cinclus cinclus</i> in southern Norway.
1997 Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (<i>Hyllobius abietis</i>), 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 soil bacteria by studies of natural transformation in <i>Acinetobacter calcoaceticus</i> .
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 responses of Arctic charr (<i>Salvelinus alpinus</i> (L.)) and brown trout (<i>Salmo trutta</i> 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 (<i>Salmo salar</i>) 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 (<i>Alces alces</i>) 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 conservation 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 <i>Strix aluco</i> : An intra- and interspecific comparative approach
1999 Hans Kristen Stenøien	Dr. scient. Botany	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 <i>Dendrocopos leucotos</i>
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 (<i>Gadus morhua</i> L.) and Halibut (<i>Hippoglossus hippoglossus</i> 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 (<i>Micromisistius poutassou</i>), haddock (<i>Melanogrammus aeglefinus</i>) and cod (<i>Gradus morhua</i>) 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 <i>Dicranum majus</i> , <i>Hylocomium splendens</i> , <i>Plagiochila asplenigides</i> , <i>Ptilium crista-castrensis</i> and <i>Rhytidiadelphus lokeus</i> .
1999 Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (<i>Salmo salar</i>) revealed by molecular genetic techniques
1999 Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from <i>Brassica napus</i> 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 (<i>Luscinia s. svecica</i>)
1999 Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (<i>Salmo salar</i> L.) and Brown trout (<i>Salmo trutta</i> 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 (<i>Cuculus canorus</i>) 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 (<i>Loxodonta africana</i>)
2000 Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (<i>Salvelinus alpinus</i>), 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 (<i>Salmo trutta</i>) 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 <i>Artemia</i> 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 forest systems
2001 Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (<i>Symphodus melops</i> 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 (<i>Rangifer tarandus platyrhynchus</i>)
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 (<i>Castor fiber</i>)
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 <i>Arabidopsis thaliana</i> and
2002 Henrik Jensen	Dr. scient Biology	Causes and consequences 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 <i>Gasterosteus aculeatur</i> 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 (<i>Syncerus caffer</i>) in Chobe National Park, Botswana
2003 Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (<i>Helicoverpa armigera</i> , <i>Helicoverpa assulta</i> and <i>Heliothis virescens</i>)
2003 Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, <i>Pogonatum dentatum</i>

2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Arctic 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 (<i>Salmo Salar L.</i>) 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 <i>Arabidopsis thaliana</i>
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 (<i>Heliothis virescens</i> , <i>Helicoverpa armigera</i> and <i>Helicoverpa assulta</i>).
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 (<i>Fragaria x ananassa</i>): characterisation and induction of the gene following fruit infection by <i>Botrytis cinerea</i>
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 Røstelién	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 (<i>Halichoerus grypus</i>) 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 <i>Echinops</i> 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 <i>Coregonus lavaretus</i> (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutants (POPs) in seabirds Retinoids and α -tocopherol – potential biomarkers 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 <i>Calanus finmarchicus</i>
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 (<i>Salmo trutta</i>) 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 <i>Syngnathus typhle</i> : 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 <i>Tenebrio molitor</i> - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hanche	phD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae