The ecology of cheetahs and other large carnivores in a pastoralist-dominated buffer zone

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“No wild animals are really bad as you will be alone without them. It is good just to see and be happy” (Iltiyogoni *laigwanan*, Loliondo).

Summary

Due to the various limitations of core-protected areas, interest in semi-protected landscapes and the human-wildlife interactions that occur within them is rapidly gaining credence. Some of the most important issues within this field are human-carnivore relationships, with many large carnivores globally threatened on one hand but with the capability of potentially devastating impacts on humans on the other. In this thesis, the success of cheetahs, their competitors and their predators in two buffer zones (Loliondo and Ngorongoro) of the Serengeti National Park in Tanzania was examined in comparison with populations living inside the park. The potential role played in carnivore ecology by the Maasai pastoralists inhabiting the buffer zones was then examined to assess the extent to which their presence determines any of the differences.

The results show that large carnivores and their prey are surviving successfully outside the core-protected area, coexisting with the pastoralist Maasai. Herbivores were shown to exist at equivalent diversity and density outside the park, with the two-year average prey biomass significantly higher in Loliondo than inside the park (χ^2_2= 49, $p<0.001$). The only species consistently more abundant inside the park were kongoni, topi and warthog. However, temporal variation was large and the system was better described as a single, dynamic entity rather than three distinct and comparable sites. Study sites outside the park also held substantial populations of all large carnivore species. Densities of both common jackal species were higher outside the park, hyaena estimates were higher inside the park and there was no significant difference between lion estimates (χ^2_2=0.4, *NS*). Lion density in Loliondo was estimated at 0.37 lions / km^2, a density comparable with most protected areas. Cheetah data were limited but showed a substantial population outside the park. Several carnivore estimation methods were used in the study, and comparison of the results showed that the visual-based surveys commonly used elsewhere (line transects or driven indices) were highly limited outside protected areas. Little behavioural variation was shown in cheetahs between individuals inside and outside the park (effect of region on time spent relaxed: $F_{5,65}$=0.09, *NS*). Both cheetahs and lions showed strong reactions to playbacks of Maasai cattle, however responses were mixed with only lions outside the park showing a consistent increase in vigilance ($T9 = -2.72$, $p<0.05$). The role of Maasai was investigated through questionnaires. Their answers showed large carnivores to be a major part of their environmental perceptions, with lions, hyaenas and leopards receiving the top salience scores, although cheetahs were not due to a lack of differentiation between the spotted cats. General attitudes were positive, particularly in Ngorongoro, but attitudes towards large carnivores were mostly negative. Costs of coexistence were significant for both sides; livestock predation was experienced by 89% of Loliondo respondents and 63% of Ngorongoro respondents, with predators accounting for 1% of cattle herds and 3% of sheep and goats, although disease accounted for far higher. Human injuries were also reported, although most (70% in Loliondo and 50% in Ngorongoro) occurred through lion hunts. The lion hunt is still an important part of Maasai culture, with over 75% of respondents reporting having attended at least one. Based on average estimates from respondents and age group leaders, 30-40 lions are thought to be ritually killed in the entire Maasai area (including Kenya) each year. However, although the relationship between the Maasai and carnivores is far from harmonious, coexistence is continuing thanks to semi-tolerant attitudes, restrictions on hunting impacts and preventative livestock management systems.

Declaration

The material contained in this thesis has not previously been submitted for a degree at University College or any other university. The research reported within this thesis has been conducted by the author unless otherwise indicated.

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Chapter 1: Introduction

1.1 *Summary*

One of the underlying practices of conservation is the allocation of land to different levels of protection, with most countries employing a range of protection levels. Partially protected areas in particular hold great interest, both in their potential for overcoming the limitations of core-protected areas and in their own intrinsic biological value resulting from the presence of humans in the environment. Of all the human-wildlife interactions that occur in semi-protected areas, human-carnivore relationships are often the most publicised and contentious, since they involve large, charismatic and often endangered species and have the potential for causing human suffering recognised worldwide. However, not all of these interactions are detrimental to wildlife. Some of the more successful groups of people to coexist with wildlife appear to be those following a pastoralist lifestyle, despite a history of conflict with conservation policies. In this section, the history of protected areas and the development of interest in semi-protected lands are described. The nature of human-wildlife conflicts that occur in such areas, with particular attention to pastoralists and their relationship with their environment is introduced, before describing the basic biology of the main players in this study; the cheetah (*Acinonyx jubatus*), the lion (*Panthera leo*), the spotted hyaena (*Crocuta crocuta*) and the Maasai people. The chapter ends by describing the potential role Maasai may play in carnivore ecology in Tanzania.

1.2 *The protected area system*

History and definitions of protected areas

The current national park movement began with calls from a Scot, John Muir, to safeguard areas of the United States, which led to the establishment by central government of Yellowstone as the first national park in 1872 (Pressey 1996) and Yosemite soon after. Since then the American model for protected areas has been adopted almost universally and the protection of land designated by central governments has become central to conservation practice; in 1985 over 500 places covering more than 425 million hectares in 120 countries were officially recognised by governments as protected (IUCN, 1985 quoted in (Hales 1989)). By 2000 there were over 30,000 protected areas world wide covering over 13.25 million km^2 of the land surface, roughly the size of China and India combined (IUCN 2002d). However, many countries vary in their definition of protected areas (Pressey 1996), so the exact estimates of protected land also vary. Currently there are six categories recognised by the World Conservation Union, of which categories I, II and III refer to areas where direct human intervention is restricted (core-protected areas), IV allows human intervention but the main goal is still conservation and classes V and VI attempt to minimise human influence on land or seascapes (semi-protected areas and buffer zones) (Table 1)

Table 1 – Categories of protected areas from (WCMC 1994). The influence of the American model of protected areas targeting areas of scenic beauty, recreation and wilderness can be seen in the official descriptions.

Category	Description
I	Strict Nature Reserve/Wilderness Area: protected area managed mainly for science of 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
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 protection and recreation.
VI	Managed Resource Protected Area: protected area managed mainly for the sustainable use of natural ecosystems.

Importance of core-protected areas

Most attention on protected areas is generally placed on core-protected areas in the categories I-III. These are areas run in the “fortress conservation” style (Adams & McShane 1992), whereby humans are almost fully excluded. This approach includes most National Parks. There is little doubt that these areas play a vital role in conservation, releasing populations from the limitations of human hunting and competition and thus supporting higher densities than would otherwise occur. The effect of human exclusion has been shown at various levels. At a general level, Woodroffe showed a simple relationship between human density and carnivore success (Woodroffe 2000) whilst Newmark demonstrated a positive relationship between human density and conflict (Newmark *et al*. 1994) (but see (Linnell *et al*. 2001)). More specifically, the benefits of individual parks have been shown, for example, suitable hunting areas just a few kilometres outside the Serengeti National Park show large gaps in large herbivore distributions when compared to inside the protected area (Campbell & Hofer 1995). Similarly, a wide range of large mammal species was shown to exist in higher densities inside the Katavi National Park in Tanzania than outside (Caro *et al*. 1998a). Core-protected areas are particularly important for species with a high economic value, for example rhinoceros (Leader-Williams *et al*. 1990) and elephants (Douglas-Hamilton 1987), both of which rely heavily upon protected areas for their survival (Western 1989). They also play a vital role as ecological baselines, demonstrating how ecological systems exist with little or no human influence, thus allowing measurement of the extent that human processes change these processes in other areas (Arcese & Sinclair 1997).

Limitations of core-protected areas

Despite their successes, fortress-run, core-protected areas also suffer many limitations. At the root of many of these problems is the fact that almost every national park created to date has followed the “fences and fines” (Wells 1992) model initially developed in America. These consist of a central government-imposed protected area which has frequently been chosen reasons such as scenic beauty, human enjoyment and entertainment (although not necessarily the enjoyment of those that wanted or needed to use the park resources) rather than biological reasoning (Mackinnon *et al*. 1986), (Hales 1989), (Heinen 1996), (Songorwa 1999). For example, of all the National Parks created in the USA, only the Everglades appear to have been created specifically to protect its flora and fauna (Hales 1989). In many cases this model is a success; many species within protected areas have sufficient space and thrive in the absence of people. Furthermore, many human neighbours of protected areas do not need to utilise their local resources and enjoy a pleasant living environment. However, in other cases the application of the same protected area model without regard to the local biological and sociological requirements can have many unforeseen consequences.

As a result, core-protected areas suffer from two primary problems. Firstly, they can suffer biological limitations enforced by their size, position and edge effects when adjoining non-protected land. Size limitation is probably the most important issue. Setting land aside for protection can be an expensive process in terms of lost revenue from other land uses, especially in poorer countries, thus limiting the size of most protected areas. However, many of the ecological processes and even individual species that protected areas are supposed to conserve can cover vast areas. For example, a recent conservation plan for grizzly bears required 34% of the state of Idaho in the US (Shaffer, 1992, quoted in Noss *et al*. 1996). Even some of the largest and most famous protected areas in the US, the Yellowstone and Everglades National Parks, are still thought to be “leaking” biodiversity (Reed Noss, quoted in Pressey 1996) despite their size and financial resources. Similar issues may also occur with the placement of protected areas, with the criteria for placement often neglecting the requirements of the species, driven instead by human demands for scenic areas, rival economic requirements for land, political decisions and national boundaries. Such issues can be particularly important in poorer countries, where protected area gazetting is less frequently driven from an internal desire to conserve and more frequently as symbolic gestures towards, or in response to demands from, the international community (O' Neill 1996). Consequently, it is frequently areas unwanted or unusable for other purposes that are gazetted as protected areas rather than the highest priority conservation locations. Core-protected areas can also suffer biologically from the effect of having a “hard” edge between protected and non-protected land. This can be a particular problem for wider ranging, larger species which come into human conflict at the park edges, frequently through direct persecution or road kills, causing higher mortality which can create population sinks (Woodroffe & Ginsberg 1998) with effects then spreading to individuals throughout the park (Parks *et al*. 2002).

The second, and perhaps most important, limitation of core-protected areas is the effect they have on human socio-economics and welfare, most commonly on the human residents on or next to the land where they are created. Again, many of these conflicts result from imposing the western park model on foreign soils, with the process initiated, driven and imposed by a central government rather than by local groups (Hales 1989). Such a concept may not be a problem in areas where few people rely on their local resources to sustain themselves, as in western countries, but the effects can be far more serious in poorer countries. For example, $203 million or

2.85% of the national GDP is thought to have sacrificed as lost agricultural revenue to the Mara conservation area in Kenya, but the profits made are not accrued locally (Bourn & Blench 1999). As a result, protected areas are frequently imposed against the will of local people and in some cases cause physical conflict. Countless examples exist in the literature of conflicts between local residents and national parks, especially in Africa. In Madagascar for example, parks are generally created against local peoples' wishes and are now suffering from heavy resource extraction from disillusioned residents (Durbin & Ralambo 1994). East Africa is the site of many of these heavy handed impositions of protected areas, with the eviction and continued conflict with previous or current inhabitants of Amboseli in Kenya and the Mkomazi and Serengeti National Parks and Ngorongoro Conservation Area in Tanzania (Western 1994), (Homewood & Brockington 1999), (Parkipuny & Berger 1993), (Arhem 1985). However, in some areas the conflict between people and parks has been recognised and addressed. For example, in the Pacific, parks created using the original models are now being re-designed and re-applied, this time using local peoples' aims and objectives and initial signs are for a much more satisfactory and stable system (Gilman 1997). Interestingly, in the west where the concept of centralised imposition of protected areas originated, protected area law is now becoming a more participatory affair. In a description of management of the North Yorkshire Moors National Park in the UK, Green (Green 1989) describes a system where local residents of the park can reject or approve changes proposed by the government, a stark contrast to the evictions of East Africa. Nevertheless, concerns over the socio-economic impact even in rich areas are still an issue, for example in North America (*e.g.* Solecki 1994) (but see Rasker & Hackman 1996), and Scotland, where accusations of "scientific colonialism" have been made as a result of imposition of some Sites of Special Scientific Interest (SSSIs) (Mather 1993).

Importance of semi-protected areas and buffer zones

It is within this context that areas where humans and wildlife live together gain importance. Buffer zones and semi-protected areas are defined as areas outside the core-protected area that are managed sympathetically, or partially protected, to minimise the impacts of outside activities (Pressey 1996) and are inhabited by both people and wildlife (Wells & Brandon 1993). Suggestions for the creation of buffer zones around core-protected areas were made as early as the 1930s in the US, although proposals were not implemented at the time (Shafer 1999). However, the concept wildlife and humans sharing a landscape dates back far beyond then. Before protected areas were introduced, human-wildlife coexistence was the norm. Even since the creation of protected areas, most still allow human activity within their borders to some extent (Caro 1999d) whilst in some areas, such as the UK, the entire protected area system is built within a cultural landscape formed and occupied by people (Green 1989). However, the limitations of core-protected areas have led to a recent increase in interest in buffer zones and semi-protected areas (Wells & Brandon 1993) boosted by an official change in interest at the 1979 Man and Biosphere Programme (Thompson 1997).

The advantages of semi-protected areas are threefold. Firstly, they hold the potential to solve many of the spatial and social problems described for core-protected areas. For example, since buffer zones and semi-protected areas do not exclude humans, the financial and ethical limitations on their size are not nearly as restrictive. Within Africa there are currently over two million square kilometres of protected land, or roughly 9% of the total surface area (IUCN 2002c). Within this, the area of partially protected areas exceeds the fully protected by 1.42:1 (Caro 1999d), therefore more than doubling the protected land available through core areas only. Furthermore, they can theoretically alleviate the problems of hard edges demonstrated by Woodroffe (Woodroffe & Ginsberg 1998) by graduating the transition from core-protected area to cultural landscapes with a heavy human presence. By considering human needs they also have the potential to solve many of problems caused by protected areas to local residents. As a result, buffer zones are the site of a wealth of community conservation programmes and Integrated Conservation and Development Projects (IDCPs) that have started in the last few years (Caro 1999d). These attempt to resolve many of the issues residents of these areas face, with varying degrees of success *e.g.* (Bell 1987), (Lewis *et al*. 1990), (Adams & McShane 1992), (Gartlan 1997), (Salafsky 1994), (Gillingham & Lee 1999), (Hackel 1999), (Infield & Namara 2001), (Adams & Hulme 2001), (Sillero-Zubiri & Laurenson 2001). At present, development in this area is still relatively new with less than 25 such projects in Africa in 1994, mostly in southern Africa, and most the subject of much debate on their success *e.g.* (Lindsay 1987) , (Patel 1998), (Alexander & McGregor 2000) and even ethics (Escobar 1995). Furthermore, there is a tendency for the pendulum to swing too far in the reverse direction, with most of these programmes concentrating most of their resources to redressing human problems as opposed to the conservation goals.

The second advantage of semi-protected areas for wildlife ecology and conservation is that they can have their own intrinsic value. In many places, the diversity of species outside national parks is equivalent to inside (Western 1989) providing important habitat for many rare and endangered species (Young 1997). However, in some cases conditions outside core-protected areas may even be superior those inside the core, providing vital habitat to a wide variety of species, just as core-protected areas do for other species. For example, there is greater diversity and abundance of small mammals outside the Katavi National Park, Tanzania, than inside (Caro 2001). Similarly, medium-sized carnivores such as wild dogs (Woodroffe *et al.* 1997) and cheetahs (Marker-Kraus & Kraus 1994) appear to be more successful outside core-protected areas in some areas where they can avoid high densities of their predators (Creel 1996), although both can also suffer conflicts with humans in the same areas (Woodroffe & Ginsberg 1999), (Marker-Kraus 1997). Various reasons have been suggested for the apparent success of many species outside of parks, with some persisting due to their value as bush meat, ecological value or for leisure whilst others may be “zero cost” species with little reason to remove, some being too rare or shy to catch and some living in areas unwanted by people. In some cases, it is simply cultural or legal reasons that ensure their existence (Western 1989).

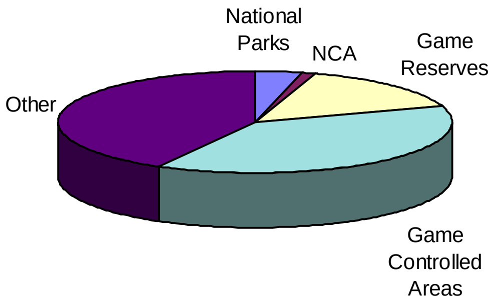
The third role semi-protected areas may play in ecology and conservation is their effect on large-scale biological processes, particularly population dynamics. Animal and plant populations are often studied as a whole (Pulliam 1988), referring to a conveniently defined, homogenous entity at a single density, whereas in reality populations occupy a heterogeneous landscape and consist of patchy sub-populations, each exhibiting its own population dynamics (Begon *et al.* 1996), (Dias 1996). This patchiness can be caused by non-human influences, such as natural variation in physical conditions, but is particularly evident when human influence is manipulated through levels of protected areas. The resulting population structure can be represented by a collection of smaller, self-sustaining populations known as metapopulations (Begon *et al.* 1996) with equivalent immigration and emigration between patches (*e.g.* (Doncaster *et al.* 1997)). However, in many cases neighbouring populations living under different conditions will vary in success, with some successful, self-sustaining sub-populations in good local environments and some unsustainable sub-populations in poor local environments that persist through immigration of the surplus from the successful areas (Dias 1996). Such a population structure is referred to as a source-sink structure and in these circumstances, sub-populations can be influenced as much by conditions elsewhere as locally (Pulliam 1988). Examples of patchy population structure and source-sink dynamics have been demonstrated in a range of wild populations, although they are notoriously hard to identify due to the difficulty in accurate measurement of the necessary demographic parameters (Pulliam 1988), (Dias *et al*. 1996) as well as the complications of pseudo-sinks (Watkinson & Sutherland 1995). Nevertheless, sources and sinks have been identified in zebra mussels (Horvath *et al*. 1996), tropical migrant birds (Donovan *et al*. 1995), blue tits (Dias *et al*. 1996), grizzly bears (Doak 1995) and are strongly suspected in tigers (Smith *et al*. 1998). Source-sink situations have many important ramifications for ecological theory and conservation but hold particular relevance for areas containing different levels of protection. Firstly, this is because the source-sink theory challenges the restrictions of the niche concept (Pulliam 1988) and shows how sub-optimal habitats may still be employed by many species, thus expanding their effective available habitat. A possible scenario may be that the core-protected area contains the optimal conditions for a species to survive and breed, and this “overflows” into a sink population that exists outside the core region. The sink population may be dependent on the source for its continuation, but its existence would increase the number of individuals in the overall population above the number predicted by the available habitat in the core area, which could have very important ecological and genetic ramifications. Secondly, the source-sink theory highlights the importance of understanding all sub-populations in a heterogeneous region. For example, research unwittingly focused upon a sink population might incorrectly identify the factors required for the population’s survival and focus conservation attention in the wrong area (Pulliam 1988). Alternatively, failure to identify a source population might lead to unwittingly isolating it or failing to protect it altogether and the subsequent decline of the sink population would be difficult to explain. It has therefore been recommended that conservation must identify productive sub-populations, protect buffer zones and marginal areas and monitor apparently stable populations carefully (Howe *et al*. 1991).

Nevertheless, despite their value in alleviating the spatial restrictions of protected areas, their potential for resolving human conflict and their likely importance in population dynamics, buffer zones and semi-protected lands are still very poorly understood scientifically (Shafer 1999) with almost nothing known of their success as conservation areas for mammals (Caro 1999d). If their potential for successful conservation is going to be realised, much more research into understanding buffer zones is required.

Protected areas in Tanzania

In Tanzania, estimates of the amount of protected land vary from 26% (Parkipuny 1997), to 19% (Job Mbaruka of Wildlife Division and the Serengeti Regional Conservation Project, Frankfurt Zoological Society and The Serengeti Regional Conservation Project 1999). 14% is said to be under IUCN classifications I-V (Thompson 1997) and 4% protected under classifications I-III (Siegfried *et al*. 1998). Of the 19% protected under the government definition, the 12 National Parks make up 4%, Game Reserves account for 15% and the Ngorongoro Conservation Area and all Game Controlled Areas (where people and wildlife coexist) make up the largest proportion at 39% combined (Frankfurt Zoological Society and The Serengeti Regional Conservation Project 1999) (see Figure 1).

Figure 1 – Division of protected land in Tanzania



Within East Africa, the importance of the semi-protected areas has been understood for some time. In Kenya the success of large ungulates outside of National Parks has been shown to be extremely high, with aerial photography showing differences only in rhinoceros, elephant and wildebeest numbers and a higher relative abundance of grazers inside parks and browsers outside (Western 1989). This importance can be further raised in areas crossed by migratory routes. For example, it has been estimated that up to 30% of wildebeest could be lost from the Serengeti ecosystem if they were restricted in their movement into Kenyan rangelands around the Mara Reserve (Norton-Griffiths 1995). Furthermore, it has been estimated that the buffer zones of Lokisale GCA and Simanjiro around Tarangire National Park provide seasonal grazing for 55,000 grazing animals, or 25% of the Arusha region's wildlife (Borner 1985) whilst buffer zones have been highlighted as vital to the future of the Manyara National Park (Mwalyosi 1991). Despite this, most semi-protected areas have no infrastructure allowing local participants to benefit from wildlife and are protected only on paper (Caro 1999d)

1.3 Human-wildlife conflict within buffer zones

Effects of humans on wildlife

Hunting

Although humans can affect wildlife in many ways, probably the most influential are direct impacts through hunting and persecution and indirect impacts through habitat loss. In the past hunting was the main impact of humans on their environment (Western 1989). In the late Pleistocene more animals were killed than at any other known time (Martin & Klein 1984), for example 30% of large mammals present in Europe were hunted to extinction, 73% in the United States, 80% in South America and 90% of large mammals went extinct in Australia during this period (Stuart 1986). In the present, hunting is no longer the major impact of humans upon their environment. However, in localised areas and on certain species it can still have major effects. Currently, hunting is generally in the form of low-level subsistence or problem animal hunting, or larger scale meat and trophy hunting. The impact of professional hunting, defined here as hunting for profit (either through sale of products or sale of hunting rights) is variable depending on the species and hunting management. For example, in Tanzania it was shown that certain small populations of eland, kudu, reedbuck and small antelopes were at risk from trophy hunting, as were lions and leopards, but most other species were unaffected (Caro *et al*. 1998b). However, professional hunting can have particularly adverse effects on high value animals. Elephant and rhinoceros hunting for ivory and horns has drastically reduced populations of both in Africa (Douglas-Hamilton 1987), (Leader-Williams *et al*. 1990), (Milner-Gulland & Mace 1991), (Caughley 1993) leaving them as two examples of species found in far higher abundance inside National Parks than outside in Kenya (Western 1989). This affect can be exacerbated for high value carnivores, which tend to live at lower density populations. For example, it has been estimated that if hunting for tiger bones continues at the current rate in Asia, many wild tiger populations will be extinct within a few years (Kenney *et al*. 1995). Since an apparently small impact through hunting can have major effects on population viability (Kenney *et al*. 1995), (Crooks *et al*. 1998), even apparently low-level hunting may still be important for conservation. Subsistence hunting probably has a lesser impact as most people who practice it are by definition limited in their access to resources such as guns and spare time; factors that can lead to major impacts. However, variable impacts do occur depending on the species, hunting method and people. For example, in Kenya a single forest was shown to display unsustainable hunting rates of large mammals and primates, but sustainable levels for smaller mammals, with trapping less harmful than active hunting (Fitzgibbon *et al*. 1996). In a study in the Serengeti, it was shown that 75,000 resident animals and 35,000 migratory animals are hunted in protected zones annually (Campbell & Hofer 1995). The off-take of buffalo, giraffe, topi and impala was particularly high but non-resident Thomson's gazelle and Grant's gazelles were relatively unaffected (Hofer *et al*. 1996). Hunting may also have an impact on non-target animals. For example, 8% of the Serengeti hyaena population is thought to be killed and 400 injured by snares annually and cats are also thought to be at high risk of accidental snaring (Hofer *et al*. 1996)

Habitat change

In historical terms the competitive effects of humans have been secondary to the effects of hunting, with habitat loss thought to be responsible for only about 20% of extinctions since 1600 (Nilsson quoted in (Western 1989)). Yet the capacity for habitat loss has increased with the world population size. Following the 1963 Technical Meeting of the IUCN where the ecology of man in a tropical environment was the chief topic, the current and future impact of man's expansion on the environment has been widely recognised (Brown 1971). Effects of habitat change, in particular conversion to agriculture, have been demonstrated for a wide range of species *e.g.* (Ratcliffe & Crowe 2001), [Robertson, 2001 #28], (Samson & Huot 1998). Effects of habitat loss and change are causing particular concern in East Africa. For example, the influx of people into wildlife areas is having serious consequences on populations in the Maswa Game Reserve due to cultivation and tree felling (Makacha 1982). Habitat loss and agricultural conversion is also thought to have a major effect on many of the migratory patterns in both the Serengeti ecosystem (Ottichilo *et al*. 2001) and nearby Tarangire (Borner 1985) and is frequently cited as the main threat to many individual East African species. For example, the main threat to cheetahs is thought to be loss of habitat (Caro 1994) partly because they are particularly vulnerable to spatial restriction since space is required for predator avoidance to be successful (Durant 1998).

Effects of wildlife on humans

Attacks on livestock

Many carnivore species have been recorded as feeding on domestic animals (*e.g.* cheetahs (Marker-Kraus 1997), cougars (Beier 1995), leopards (Mizutani 1993), (Sekhar 1998), tigers (Sekhar 1998), wild dogs (Rasmussen 1999)), with the wildlife responsible generally determined by the size of the livestock; in Kenya, lions, followed by hyaenas and leopards accounted for most cattle predation. Hyaenas, followed by leopard, cheetah, jackal and wild dog preyed on sheep and goats (Mizutani 1993). The reasons for wildlife preying on livestock vary and are not fully understood. In some areas, it is thought that individual animals learn that livestock are easier to catch or are forced to switch prey species due to depletion of their natural prey choice (Mizutani 1993). In others, predation may occur simply because there is nothing to prevent it, for example in Namibia much livestock is not herded as it is in many other African areas and as a result, cheetahs frequently take livestock or game species (Marker-Kraus 1997). Experience and sex may also be influential, with a study of lion predation in Gir Forest, India, showing a disproportionate number of attacks due to sub-adult lions (Saberwal *et al*. 1994), whilst male tigers are more likely to cause problems than females (Sukumar 1991). There is also some evidence that much predation is due to one or two individuals only in a population due to learnt behaviour (Frank & Woodroffe 2001) (but see (Linnell *et al*. 1999)).

Attacks on people

Threat of personal injury due to large carnivores is one of the key concerns of people living with wildlife, as illustrated by a survey of community conservation programmes, which showed 88% of respondents recording it as a concern in their area (Sillero-Zubiri & Laurenson 2001). Such concern does not represent actual levels of attacks, with human injury or death a relatively rare occurrence; however, it demonstrates that even a low actual impact can have a large impact on local perceptions. Nevertheless, although rare, attacks on people do regularly occur. One of the main areas for human attacks by carnivores is Asia. Tigers are the main culprit, with populations frequently overlapping with high-density human populations *e.g.* (Nepal & Weber 1995b), (Sukumar 1991). However, the single Asian lion population in the Gir Forest of India also causes major problems for people, with a population of about 250 lions responsible for an average of 15 attacks and 2 human mortalities per annum between 1978 and 1991 (Saberwal *et al*. 1994). Attacks by lions are also regularly reported in Africa *e.g.* in the Luangwa Valley, Zambia, where a small pride was excluded from the National Park by larger prides and forced into coexistence with people (Yamazaki & Bwalya 1999). One of the most famous man-eating episodes in history also involved lions in Tsavo, Kenya, at the end of the 19th century, when over 100 people were killed (Patterson, 1907, reported in (Sillero-Zubiri & Laurenson 2001)). Although the carnivores responsible for most direct interactions with people are tigers, lions and mountain lions (Sillero-Zubiri & Laurenson 2001), other species also attack occasionally. For example, in one recent attack a sleeping boy was attacked by a spotted hyaena in northern Kenya, losing his nose (Flying Doctors Society of Africa 2002). Other stories of hyaenas include an attack on an elderly patient at Shinyanga hospital in Tanzania or regular attacks on sleeping people or children in Malawai (Kruuk 1972). Two similar reports come from Loliondo in Tanzania. The first was reported on 22 January, 1968 in the Tanzania Standard, describing hyaenas biting over 60 people, mostly women and children (Kruuk 1972). The second occurred in 1999 at the village of Olorien, one of the villages in this study, when a hyaena subsequently discovered to be rabid attacked several people, including a young girl who needed major plastic surgery provided by the Flying

Doctors. Nevertheless, the threat from most carnivores is very low. For example, there is no record of a cheetah ever having killed a human in the wild (IUCN SSC Cat Specialist Group).

Competition for crops and grazing

Wildlife can also cause many problems by either competing for natural resources or by eating crops. The latter can be particularly important in predominantly agricultural areas, depending on the proximity to wildlife areas and types of crops grown (Hill 1997) with common culprits including bush pigs, baboons (Hill 1997) and elephants (Sukumar 1990), (Sukumar 1991), both in Asia (Nyhus *et al*. 2000) and in Africa (Abel & Blaikie 1986), (Hoare & Du Toit 1999), (Hoare 2000). Crop raiding can be a major factor in crop losses. In a study in India at least half of all damage to crops was caused by wild animals (Sekhar 1998). This can in turn increase the impact of humans on wildlife by adding reason to hunt them (Fitzgibbon *et al*. 1996).

Disease interactions

Disease interactions can be particularly harmful, primarily affecting humans by infecting their livestock. In the Ngorongoro Conservation Area (NCA), Tanzania, disease interactions are thought to enable wildlife to out-compete cattle at certain times of the year due to the risk of transmission of various diseases. Most important in the NCA is Malignant Catarrh Fever (MCF), which is transmitted from calving wildebeest to cattle grazing in the same area. In the worst cases the presence of wildebeest can keep people away from their preferred grazing areas for up to six months of the year (Machange 1997).

Pastoralists and wildlife

General perceptions of pastoralists

Pastoralist people are generally defined as those who depend wholly or almost wholly on products from livestock. They seldom eat agricultural products and when they do, they are usually traded, not grown. Indeed, they often regard cultivators as inferiors (Brown 1971). Many groups exist world-wide with an estimated 50 million living south of the Sahara, including the Fulani, Tuareg, Maasai, Somali, Boran and Danakil groups (Brown 1971). Despite the fact that no large mammals have become extinct in 3000 years of coexistence with pastoralists (Western 1989), historically pastoral people have been seen as a threat to wildlife conservation, either due to the impact of their livestock-based lifestyle or their hunting activities, and have even been seen as an obstacle to national development (Collett 1987), (Howell 1987). Various reasons appear to influence these attitudes, including the incompatibility of a nomadic lifestyle with conventional attitudes on service provision, an apparent wastefulness of land potential and their representation of out-dated, tribal systems (Howell 1987), although there are suggestions that a more deep rooted fear of things different drives much of settled people's prejudices for pastoralists and nomads (Monbiot 1994). For example, Brown (1971), refers to the "generally accepted view that cultivation of crops is a more highly evolved...form of livelihood than is pastoralism". In East Africa a large influence in this perception appears to be the legacy of colonial administration. For example, early accounts describing the Maasai as aggressive people, obstructing the path to development and wasting the potential of their land for agriculture were actively used by the British colonial government to promote the annexation of the East African Protectorate and to resettle their lands with white agricultural farmers in the first half of the 20th Century (Collett 1987). The perception of pastoralists as unnecessarily warlike, wasteful and ignorant and requiring western guidance persisted into the 1970s with descriptions of an "ecologically unwise" reliance on milk, the destruction of habitat "without being driven to do so" and the comment that "unless controlled, they kill each other and steal each other's stock" (Brown 1971). Misunderstandings based upon the western view of how land should be used most profitably fuelled the conflict and persist today (Behnke & Abel 1996). Whereas maximum growth per animal may be a suitable goal for western cattle farmers, pastoralists inhabiting unpredictable rangelands may view the acquisition of a wide range of livestock products and the security offered by a larger herd as preferable goals (Homewood & Rodgers 1987). In the 1950s, such a conflict of views drove the introduction of services in an attempt to force the Maasai into a more conventional, sedentary ranch-style life (Collett 1987). Then, as wildlife conservation became more fashionable at the end of the colonial period, the Maasai were seen as potentially harmful to the new goals and challenged on moral grounds. For example, a 1961 UNESCO report argued that the Serengeti National Park "and its marvelous fauna were being gravely threatened...largely by the rapidly increasing Masai" whose cattle were "ruining the grazing and water-supplies on the migration route along its edge" (Huxley, quoted in (Collett 1987). Prejudice towards pastoralists still persists today, partly due to their minority position. Most of the population of Kenya and Tanzania, for example, originate from arable agriculture social backgrounds. Thus the arable bias is highly influential in the national perception of development; increasing the land under cultivation has become synonymous with development, pastoralism with backwardness (Parkipuny 1997).

Pastoralism and overgrazing

The general perception of pastoralists is often supported with evidence of their environmentally destructive and wasteful lifestyle. Common accusations include the view that pastoralists overgraze the land, redistribute nutrients, trample vegetation, spread disease and kill the wildlife. For example, many inhabitants of the Usungu Plains in southern Tanzania believe the recent influx of Wasakuma pastoralists has led to overgrazing and consequent bush encroachment, overcrowding of the land and an increase in livestock diseases (Charnley 1997). Some argue this is due to mismanagement inherent in the pastoral lifestyle *e.g.* (Lamprey 1983), others suggest it is due to external pressures such as restrictions on movement and land use (Sinclair & Fryxell 1985), (Charnley 1997). However, although it is generally acknowledged that pastoralists can *potentially* cause environmental damage, the general perception of the *actual level* of destruction also appears to be based on conventional wisdom and inbuilt prejudice, sometimes with little basis in fact (Homewood & Rodgers 1987). Overgrazing is defined as occurring when there is vegetation change and an accompanying loss of animal productivity attributed to grazing by herbivores (Wilson & MacLeod 1991). Range degradation through overgrazing by pastoralist livestock is often attributed to the “common property problem” whereby land is owned communally. This can encourage overstocking by individuals (Livingstone 1991) or lead to overstocking for increased social prestige (Brown 1971) and there are many examples of studies showing the detrimental effects of overgrazing. For example, enclosures protected from livestock in Saudi Arabia showed large increases in total cover and species richness (Shaltout *et al.* 1996) whilst overgrazing was one of the explanations given for massive land loss in Maasailand (Mwalyosi 1992) and the desertification of the pastoralist Samburu District in Kenya (Kasusya 1998) and in the Sahel (Sinclair & Fryxell 1985). Over-population and the resultant increase in cattle has been suggested to explain land degradation in the Baringo District of Kenya whilst prestige overstocking was held to blame in the Kajiado District (Brown 1971).

Although overgrazing undoubtedly can occur, with countless published accounts, a high cattle density does not necessarily lead to overgrazing *e.g.* (Sandford 1982), (Homewood & Rodgers 1987), (Ellis & Swift 1988), (Behnke & Scoones 1993), (Baars *et al*. 1997). Rather, the evidence that is used to support overgrazing theories is often masked by the high levels of fluctuation common in the unstable rangeland environments pastoralists inhabit *e.g.* (Livingstone 1991). For example, natural fluctuation of vegetation growth patterns due to variation of rainfall from year to year can often be higher than the differences observed in short term grazing-exclusion experiments (Homewood & Rodgers 1987). Theoretical models show rangelands have many features that give high resilience to such fluctuation including increased growth rates at low biomass, spatial heterogeneity that gives rise to herbivore migration and plant refuges, underground plant reserves and plant dormancy (Homewood & Rodgers 1987). Furthermore, pastoralists are often labeled as overstocking, even possessing a “cattle-complex” (Collett 1987) and exceeding the carrying capacity of their land. Yet the concept of carrying capacity applied to such an unstable environment may itself be flawed (McLeod 1997), and there is evidence that the pastoralist stocking strategy of following the fluctuations in the environment is more efficient than a set stocking level carrying capacity (Homewood & Rodgers 1987).

Hunting

Evidence for direct impacts of pastoralists on wildlife through hunting is particularly scarce. On the contrary, archeological evidence from the Serengeti region, Tanzania, shows that pastoral people have coexisted with wildlife for at least 2,500 years and that wildlife was generally only used directly in times of drought or hardship (Collett 1987). In fact, many pastoralist people show an active avoidance of killing, the Bisnoi of North East India being an extreme example (Kemf 1993). Although pastoralists do not generally hunt, conflict does occur between livestock and carnivores, which can lead to killings through hunting or poisoning. For example, the Tuareg people of Niger show little interest in hunting, but have been recorded to leave strychnine-laced carcasses to kill jackals and striped hyaenas in defence of livestock (Kemf 1993)

1.4 Cheetahs and other large carnivores

Global carnivore status

Large carnivores are currently one of the taxa declining most quickly today, due to habitat loss, hunting, prey depletion, disease and trade in body parts (Wikramanayake *et al*. 1998), (Novaro *et al*. 2000), (Sillero-Zubiri & Laurenson 2001). Reasons for persecution are too numerous to go into detail, but include self protection, protection of prey populations , sport, consumption in medicines, as reservoirs of disease or simply because they are disliked *e.g.* (Smith *et al*. 1997), (Heydon *et al*. 2000), (Frank & Woodroffe 2001). In many countries such as the US the declines have been especially drastic over the last 200 years as new weapons have been introduced (Frank & Woodroffe 2001) and in others, such as Britain, large carnivores have been completely exterminated (Sillero-Zubiri & Laurenson 2001). Part of the reason for their vulnerability is their ecology, with most species never existing at high densities due to their position at the top of the food chain or as keystone species (Noss *et al*. 1996) and each requiring a large area to live which frequently brings them into contact with humans (Woodroffe & Ginsberg 2000). Reproductive ecology for most species involves long gestation periods, small litter sizes and delayed sexual maturity making population recovery slow (Sillero-Zubiri & Laurenson 2001), although there is great variation of susceptibility due to variation in life history within the taxa, for example wolves are some of the most resilient in the US, grizzly bears the least (Weaver *et al*. 1996). Understanding large carnivore conservation biology is essential (Weber & Rabinowitz 1996), partly due to their vulnerable nature, partly because of their role as ecosystem indicators and partly for their potential role as “umbrella species” (Noss *et al*. 1996), but see (Linnell *et al*. 2000), with their successful conservation automatically incorporating many other species (Sillero-Zubiri & Laurenson 2001). Furthermore, with the move towards conservation in human landscapes, carnivores represent one of the most difficult challenges to surmount, causing a range of problems for humans.

The cheetah

Physiology and phylogeny

The cheetah is a medium-large cat, with females weighing an average of 35.9 kg and males 41.4 kg (Caro 1994). Genetic analysis suggests that cats have diversified in three main lineages, with the cheetah (*Acinonyx jubatus*) occupying the pantherine lineage together with lions, tigers and lynxes, and that their relatively unusual morphology has arisen within the last two million years (Caro 1994). With the exception of a small population in Iran (Jackson 1998) there is scant evidence of cheetahs outside Africa. The main remaining populations exist in southern and eastern Africa (Caro 1994).

Social organisation

Social organisation of cheetahs has been a much-debated topic. In South West Africa group sizes of up to 14 animals have been reported, which is at least six animals more than the largest recorded litter size, and evidence was reported of female sociability (McVittie 1979). However, much confusion exists over reports of cheetah groups leading to mistaken records of social adult groups. This is partly due to the fact that cheetah cubs may still be with their mother even when they have outgrown her, giving the appearance of a group of adults. Furthermore, adoptions of nearly adult cubs by unrelated families can occur, mothers and young may occasionally join in temporary social groups and consorting adults may give the appearance of mixed sex sociality (Caro 1994). Long-term study in the Serengeti with individually recognised cheetahs have now solved this issue, showing that females and males have different social systems (Caro 1994), (Frame & Frame 1981). In the Serengeti, females are solitary. However, there is little evidence for avoidance; they do not control or defend territories, instead inhabiting large, overlapping ranges of an average 833km^2, which follow the movements of Thomson’s gazelle, their main prey (Caro 1994). Consequently, they tend to occupy the southern short grass plains in the wet season and north western areas in the dry (Durant *et al*. 1988).

In contrast, males can be social or solitary. Two different studies in the Serengeti have estimated the proportions of each: Frame and Frame (1981) found 66% were single, 27% were pairs, 7% were trios, whilst Caro and Collins recorded 47% lived alone, 38% in pairs and 16% as trios (Caro & Collins 1987b). Occasionally groups of four or five males have been recorded (Caro & Collins 1987a), (Durant, pers. ob.). Pairs are usually littermates whilst trios and larger often include an unrelated male. It appears the main advantage of sociality for males is the associated increase in ability to defend a territory and territory holders are more likely to be social than solitary (Caro &

Collins 1987a), (Caro 1994). Defence of territories is fierce and there are accounts of cheetahs being killed in such fights (Caro *et al*. 1989), although territories cannot be exclusively defended and other males do pass through (Caro 1994). Territory sizes average 37.4 km^2 and do not appear to have any particular ecological characteristics, apart from the presence of cover and the fact that they hold high numbers of Thomson's gazelles when occupied and were abandoned when prey levels fall (Caro & Collins 1987a). However, territories in the Serengeti have been sited in specific locations for long periods, despite changing tenants, and large areas have never been occupied (Caro 1994). These areas are thought to be favoured "hotspots" for contact with females, with more females sighted in territories than in areas unoccupied by territorial males (Caro 1994). Once a receptive female is found within a territory, access to her and mating appears to be shared equally between all territory holders, although few matings have actually been witnessed (Caro 1994).

Non-territorial males or "floaters" follow an alternative strategy to territory defence, ranging over areas averaging 777 km^2 (Caro 1994). Often non-territorial males are singletons or young siblings (Caro 1994). Access to females does not appear to be any different for non-territorial males compared to territorial (Caro & Collins 1987b), however, non- territorial males are in significantly worse condition than territorial males, suggesting that non-territoriality is a less favourable strategy (Caro *et al*. 1989).

Feeding ecology

Cheetahs are diurnal and hunt during the day (Caro 1994). Various strategies are employed including stalking, approaching prey in full view and flushing hidden prey from long vegetation (Caro 1994), all utilising the cheetah's exceptionally high running speed. Hunting success is high with 54% of adult gazelle hunts and 100% of neonate fawn hunts being successful (Caro 1994). Preferred food of cheetahs varies with location. For example, on the Serengeti plains, Thomson's gazelles are the preferred prey, whilst impala are favoured in South Africa and puku in Zambia (Caro 1994) although most preferred species weigh less than 40 kg (Schaller 1972a). Furthermore, preferences may differ between sexes, with no records of females in the Serengeti ever having taken an adult wildebeest, whilst male groups frequently target them (Caro 1994). However, both males and females tend to target young animals.

54% of Thomson's gazelles targeted by Serengeti plains cheetah are young despite them constituting just 6% of the population (Fitzgibbon & Fanshawe 1989).

Reproductive ecology

Female cheetahs in the wild breed from about two years (Kelly & Durant In press). Males are sexually mature at around the same time (20-23 months) (Caro & Collins 1987b) but rarely breed until after approximately three years in captivity (Caro 1994). Little is known of courtship behaviour since it has rarely been witnessed in the wild (Caro 1994). However, it is thought that a male will consort with a female for approximately two to three days, primarily mating at night at up to eight hour intervals (Caro 1994), (Frame & Frame 1981). Most successful conceptions are made during the wet season, although there is no seasonal peak in births (Caro 1994). Gestation is between 90 and 95 days and the average litter size is 3.6 (Laurenson 1994). The maximum litter size recorded is eight cubs, although litters rarely exceed six in the wild (Caro 1994). This is a relatively large litter size compared to other cats, with only the European wildcat and Pallas' cat known to have larger average litter sizes, which could be an adaptation to high cub mortality (Caro 1994). Cubs are born in a lair, which is usually a hidden area in marshy or thick vegetation, gullies or kopjes where they remain for an average of 8.2 weeks, with the mother moving the cubs every 5-6 days (Laurenson 1993). Once the denning period is over, cubs will join their mother on hunts and eat solid food, however nursing will continue for about four months (Caro 1994). Compared to other felids, cheetah cubs have a high growth rate which is thought to be a further adaptation to high predation risk (Laurenson 1995a).

Young cheetahs are extremely dependent on their mother for a long period, staying with them for between 13-20 months (an average of 18.2 months) whilst they reap the benefits of her superior hunting skills and all benefit from increased vigilance levels and reduced harassment from hyaenas and other cheetahs (Caro 1994). Most leave in the wet season, presumably due to higher prey levels, yet even so their hunting success and food intake is initially very poor (Caro 1994). After separation, littermates of both sexes stay together for an average 6.7 months (Caro 1994). After this period females will separate from their male siblings whilst males will stay together for life (Caro 1994).

One of the striking features of cheetah reproductive ecology is the exceptionally high level of cub mortality shown in several studies. Schaller (Schaller 1972b) found one third to one half of deaths occur within three months of leaving the lair whilst Burney (Burney 1980) found 41% died in the same period. In a comprehensive study in the Serengeti the following breakdown of cub survival was calculated:

Table 2- Cub mortality (Laurenson 1994))

Time period	Cubs born into lair	Surviving to 8 weeks (emerge from lair)	Surviving to 4 months	Surviving to 14 -18 months
Number of cubs	125	36	10-12	5-7
Percentage of total	100	28.8	8-9.6	4-5.6

Such figures put cheetah juvenile mortality higher than any other non-hunted felid (Caro 1994). Overall, cheetah cubs have only a 4.85% chance of survival to independence (Laurenson 1995b). The causes of mortality of cubs in the lair in the Serengeti study are summarised below, showing that predation is by far the most influential factor on this stage of cheetah life history:

Table 3 - Causes of cub mortality (Laurenson 1994)

Cause	Percentage of known deaths
Predation	73.2
Abandoned	8.2
Fire	8.2
Exposure	6.2
Inviable cubs	4.1

The primary predator at this age is the lion (see below) with no association between hyaena presence and the reproductive success of cheetah mothers with cubs, however golden jackal presence has also been correlated with cheetahs with cubs and it has been suggested this requires further investigation (Kelly 1998). It has been argued that these results may have been influenced by the research car attracting predators to the lair, or that such high rates of mortality are because whole litters tend to get killed whenever discovered (O'Brien 1994). However, the effect of handling and observation were investigated but not found to be influential (Laurenson & Caro 1994) while analysis of mortality using whole litters as the unit of analysis, still found that 67% of litters were predated (Laurenson *et al*. 1995b).

Interspecific influences

One of the main influences on cheetah ecology is other carnivores, which have a major impact on cheetah distribution, behaviour and reproductive success. Various predator species can potentially affect cheetahs; however, lions and hyaenas appear to have the major impact as shown in five different ways:

1. Cheetahs in areas with lower lion presence are sighted with larger litter sizes, with Namibian cheetahs having a mean litter size at 10 months of 4, double the Serengeti value (Kelly 1998).
2. Cheetah and lion biomass across nine protected areas are negatively correlated when controlling for prey biomass (Laurenson 1995b). Cheetah sightings in Namibia are also inversely proportional to sightings of other predators (McVittie 1979).
3. Cheetahs seen more frequently close to lions have a lower reproductive success than cheetahs seen less frequently in the presence of lions (Kelly 1998).
4. Cheetah ranging patterns show avoidance of areas with high densities of their favourite prey, Thomson’s gazelles, apparently because these are the areas favoured by lions and hyaenas (Durant 1998). The avoidance of hyaenas is strong at high hyaena densities and lion avoidance at all densities, although lion avoidance is restricted to behavioural and local avoidance since lions are less clumped than hyaenas (Durant 1998). A similar effect is shown on wild dogs which occur in higher densities in areas where hyaenas and lions are more scarce (Creel 1996) (Mills & Gorman 1997).
5. Playback experiments of lion roars and hyaena whoops show cheetahs moving away from playback sites (Durant 2000a).

There are three likely reasons for cheetah avoidance of these predators. Firstly, both lion and hyaenas are known predators of cheetahs (Caro 1994). For lions, this is particularly true for cheetah cub killings (see above) where they are responsible for 78% of all recorded juvenile cheetah predation (Laurenson 1994). However, hyaenas are thought to be equally important predators after cheetah cubs have left the lair (Laurenson 1995b). Both lions and hyaenas have also been recorded to kill adult cheetahs (Caro 1994), although data on causes of adult deaths are hard to obtain in the field and little is known on the causes of most adult mortality. The effects of cub predation on cheetah success have been described, but PVA (Population Viability Analysis) has suggested adult mortality could be even more important for population viability than juvenile mortality (Crooks *et al*. 1998). This has been disputed, however, by Kelly and Durant (Kelly & Durant In press) who show that, despite the high sensitivity to adult mortality, cheetah populations are most likely to suffer from the impact of fluctuations of juvenile mortality.

The second impact of large carnivores on cheetahs is through kill stealing. Kleptoparasitism of cheetah kills by larger predators is well recorded *e.g.* (Caro 1994), (Schaller 1972b), (Stander 1990) and a recognised foraging strategy of lions and hyaenas is to use descending vultures as a cue to locate kills (Kruuk 1967). Losses of cheetah kills to scavengers on the Serengeti plains were estimated at 9% (Frame & Frame 1977), 14% (Schaller 1972a) and 12.7% (kills spotted) or 9.2% (flesh lost) by Caro (males only) (Caro 1994). This compares to 2% recorded for leopard losses (Stander *et al*. 1997). Hyaenas are by far the more common scavenger, but both lions and hyaenas can usually drive singletons and groups of both sexes of cheetahs from their prey on most attempts (Caro 1994). The impact of such losses is unlikely to be major, but it is sufficient to influence the hunting behaviour of cheetahs since cheetahs will often move kills into cover, consume them quickly and move away from the area after finishing (Durant, unpubl.) (Maddox, pers. ob.). Furthermore they have been observed to give up hunting if hyaenas were seen or lions heard (Caro 1994) and playback experiments have demonstrated that cheetahs are less likely to hunt if they have heard either predator (Durant 2000a). The importance of competition at kills from other predators has also been illustrated for wild dogs by Creel and Creel (Creel 1996) who showed that in areas that wild dogs had high competition at kills, such as the Serengeti or Ngorongoro, they were relatively unsuccessful. However, in areas of lower competition due to hyaenas being more nocturnal, dog packs being very large or dogs moving out of the park away from the larger predators, the dogs were far more successful. Kleptoparasitism may not have a major impact on cheetah ecology, however it may still cause range restriction or force them into areas of low prey density.

Thirdly, larger carnivores may also affect cheetahs through competition for food resources. Such indirect competition is difficult to assess (McVittie 1979), however a considerable overlap of prey taken by the large carnivores does occur (Kruuk 1967). For example, in the Serengeti lions feed on wildebeest, zebra, Thomson's gazelle, buffalo and warthog in decreasing proportions whilst hyaenas feed on wildebeest, Thomson's gazelle, zebra, Grant's gazelle and kongoni (Kruuk 1967). Cheetahs feed on Thomson's gazelle, hares, wildebeest and Grant's gazelle (Durant 1998). The level of overlap may even be increased on the plains where lions take smaller prey than in the woodlands (Kruuk 1967) or when prey is short and lions focus more on Thomson’s gazelles (McVittie 1979). However, in the Serengeti there is no evidence that cheetahs are limited by prey; in contrast prey scan data show there is no significant association between food availability and reproductive success of cheetahs (Kelly 1998) while Laurenson (Laurenson 1995b) has shown that the Serengeti biomass of prey is higher than required to support equivalent cheetah populations elsewhere. Even during the litter-raising period, potentially the most vulnerable time due to decreased mobility, lack of prey has a low impact, with only 7.7% litter failures found to be related to food shortage (Laurenson 1994).

Conservation status

In 1975 the worldwide cheetah population was estimated to be 7,000 to 23,000 (Myers 1975) with Namibia holding the most, estimated at 2,500 (Marker-Kraus 1997). Tanzania is estimated to hold approximately 500-1000 (Gros 2002). Few continuous populations number above two hundred and fifty (Caro 1994). It is suspected that numbers have fallen since this time, with the Namibian population thought to have halved since the mid-eighties (Marker-Kraus 1997), and evidence of reductions in Malawi (Gros, no date). However, there are insufficient data for a new world-wide estimate (Caro 1994). Nevertheless, the cheetah is listed on Appendix I of the CITES Red Data Lists and classified as “Vulnerable” (Caro 1994). Cheetahs naturally live at low densities, ranging from 0.25 to 5 per 100km^2 (Myers 1975) however, local densities can fluctuate greatly (Caro 1994). Consequently, the human impact can be severe. Human activity is thought to be the main factor threatening cheetahs. The relationship between humans and cheetahs stretches back several hundred years, with cheetahs taken as hunting animals by Arabs, Abyssinians and Mogul Emperors in the sixteenth century (Frame 1984), but in modern times the principal threat to cheetahs world-wide is habitat loss, principally to cultivation (Caro 1994), (Marker-Kraus 1997). Hunting may also be a factor and is permitted under

CITES in Namibia, Zimbabwe and Botswana with 1992 quotas set at 150, 50 and 5 respectively, but in most other countries the cheetah is protected (Caro 1994). Non-tourist hunting and trapping also still occurs (Marker-Kraus 1997), although in comparison to other carnivores cheetahs are relatively hard to kill since they do not return to kills, making them less susceptible to poisoning, which is a common form of predator control (McVittie 1979). Nevertheless, trade is not illegal in some European countries and Japan and an estimated 5000 skins were traded annually in the 1980s (Frame 1984). The cheetah conservation status, and in particular their status in captivity, is not helped by their low genetic diversity. Comparing 47 allozyme loci, O'Brien (O'Brien *et al*. 1983) showed that South African cheetahs from two different populations exhibited heterozygosity levels of just 0.013, dramatically lower than levels found in other cats and mammals in general. However, the significance of the heterozygosity levels compared to ecological factors for the species' survival and conservation purposes is hotly debated (*e.g.* see (O'Brien 1994), (Crooks *et al*. 1998), (Laurenson *et al*. 1995a)).

The lion

Physiology, phylogeny and distribution

The lion (*Panthera leo*, Linnaeus, 1758) is the largest African carnivore, adult males recorded in a Serengeti study weighing an average of 189 kg, with females slightly smaller at 126 kg (Pusey & Packer 1987). Although formerly distributed across Europe, Asia and throughout Africa (Estes 1991), (Packer & Clottes 2000) lions are now limited to the African continent and a single population in Gir, India (Van Orsdol *et al*. 1985), (Saberwal *et al*. 1994). Within Africa they can occupy most habitats excluding rain forests and deserts (Estes 1991), although some lions in Namibia have been recorded in desert conditions (Stander 2001).

Social organisation

Lions are gregarious, social animals and may either exist within prides or as solitary nomads (Schaller 1972b). Prides can be comprised of up to 37 individuals, but this is rare and typically number 10-20 in the Serengeti, comprising mainly of females and cubs accompanied by 1-6 males (generally 2-3) (Schaller 1972b), although members of the pride may fragment into smaller groups within the home range (Packer & Pusey 1983a). All pride members are strongly territorial, defending their home range from same sex intruders, with pride home range varying from 2000km^2 in Namibia (Stander 2001) to average home range sizes in the Serengeti of approximately 200km^2 (Schaller 1972b), although ranges are not fixed across time and lions will follow prey distributions to some extent.

Feeding ecology

Lions are only active approximately 15% of the time, with most hunting activity occurring early or late at night. Since lions are limited to less than 60 kph and are unable to maintain speed for more than 100 metres, hunting strategies differ from the cheetah, with a high dependence on stalking (88% of hunts in the Serengeti) to within 30m of the prey before chasing. The majority (85-90%) of hunting is undertaken by the less conspicuous females, with approximately half involving more than one lion. Hunt success is lower than for cheetahs, with about 18% of solitary hunts successful and 30% of communal hunts successful (Schaller 1972b). The dietary preference of lions is for medium sized and large ungulates, weighing between 50-300kg, including wildebeest, zebra, and buffalo (Schaller 1972b), with larger prey tending to be taken during communal hunts. However lions will take a range of food items, including rodents and reptiles when food is scarce. Scavenging is also an important part of feeding, accounting for about 10% of total carcasses seen feeding on, but up to 40% of certain species (Schaller 1972b).

Reproductive ecology

Since females are a clumped resource the main male strategy is to try and monopolise several females, therefore sexual dimorphism is high. Since male coalitions are more successful than a solitary male for gaining access to and defending a pride, male litter mates will usually stay together and form coalitions. Most coalitions are small, usually in pairs, but in the Serengeti, a coalition of seven males has been recorded (Packer *et al*. 1988). In addition, unrelated males will often band together with 42% of coalitions in the Serengeti including one or more unrelated individuals (Packer & Pusey 1982). Pride tenure is a high risk and high stress occupation for males and tenure rarely lasts more than two years, with tenure time correlated with coalition size (Bygott *et al*. 1979). To maximise individual reproductive success males will kill current and immediately subsequent cubs when a pride is taken over which causes the females to come into oestrus (Hanby & Bygott 1987). Following such take-overs females demonstrate reproductive synchrony, facilitating communal care of the cubs within the pride. At other times, breeding is non-seasonal, but tends to be synchronised within prides (Packer & Pusey 1983b). During breeding, many copulations are required to induce ovulation and when females are in oestrus copulation rate averages about 2.2 per hour for up to six days (Packer & Pusey 1983b). Gestation is approximately 110 days and before birth to 1-6 (average 2.3 in the Serengeti) cubs in a hidden lair (Schaller 1972b). Although initially separate from the group, little effort is made by the mother to actively exclude the rest of the pride from her young (Schaller 1972b) and within about seven weeks cubs can keep up with the rest of the pride. Cubs are weaned at about 7-9 months, joining in hunts at 11 months, but unable to fend for themselves before 16 months (Schaller 1972b). Cub mortality is high, calculated at a minimum of 67% in Schaller's study, resulting from starvation as a result of low prey abundance, infanticide during change in male tenure, predation from spotted hyenas and disease (Schaller 1972b). If cubs survive, males are usually forced out of the pride aged 2-3 years (Hanby & Bygott 1987) before reaching maturity at about 5 years old whilst females remain in the group unless resources are limiting, reaching sexual maturation at about four years (Pusey & Packer 1987). Between dispersal and joining a pride, immature males and emigrant females tend to be nomadic, commonly forming associations with same sex individuals (Hanby & Bygott 1987).

Conservation status

Although the range and populations have decreased, lions are still relatively abundant in Africa, and are frequently the second most numerous predators after the spotted hyaena (Estes 1991). However, lions are frequently the most common carnivore to come into conflict with people (see "Attacks on livestock", p.25 and "Attacks on people" p.26) and consequently do not usually survive successfully in close proximity to humans. However, humans have always had a fascination with cats, portraying them in heraldry, on flags or emblems and are generally associated with positive attributes (Kruuk 1972) such as "lionhearted" or "feline grace". Consequently, the predatory cats do not seem to stir the same bad opinion as do wolves, hyaenas and other dog-like species (Kruuk 1972), (Kellert *et al*. 1996). In Tanzania, lions are classed as "low risk" in National Parks by the IUCN threat status categories but "vulnerable" in areas exposed to hunting (Bauer *et al*. 2001).

The spotted hyaena

Physiology, phylogeny and distribution

The spotted hyena (*Crocuta crocuta*) is the largest of four extant species of the Hyaenidae family and numerically is the most abundant large carnivore in sub-Saharan Africa occupying most habitat types although less common in rainforest (but see (Sillero-Zubiri & Gottelli 1992)) or arid habitats. Although spotted hyaenas diverged from striped hyaenas approximately ten million years ago (Savage, 1978 cited in (Estes 1991)) both evolved into similar body shapes well adapted for scavenging.

Social organisation

Spotted hyenas have variable social organisation depending on spatial and temporal availability of prey. When food is scarce, hyaenas demonstrate solitary behaviour, but usually are gregarious, forming territorial, hierarchical, female led clans of up to 80 adults. Unlike lions, there is no communal care of young and females compete for access to resources. This competition for dominance and access to resources has been suggested as the explanation for larger female size and aggressiveness; females weigh an average of 55.3 kg compared to males which weigh an average 48.7 kg (Kruuk 1972). Higher-ranking alpha females and males have greater reproductive success, and rank passes advantages onto offspring. Females tend to remain within the clan, whereas males disperse at around 2 years.

Feeding ecology

Activity is predominantly crepuscular and nocturnal, with two peaks in the late evening/early night and around dawn, during which feeding, hunting and social behaviour occurs (Kruuk 1972). The diet of spotted hyena mainly consists of ungulates, which are either scavenged or hunted, with scavenging accounting for 20% (gazelle fawns) to nearly 70% (zebra foals) (Kruuk 1972). Although usually foraging alone or in pairs, others may opportunistically join a hunt and occasionally co-operative hunts may occur (Estes 1991). Hunting techniques involve identifying a young or weak animal by causing the herd to run and separate. (Kruuk 1972). What hyaenas lack in speed they make up for in endurance and prey exhaustion is the usual cause of success. They are efficient feeders consuming virtually all parts of the prey including the bones (Kruuk, 1972). Competition at kills is high and noise will attract more clan members. Feeding is rapid with hyenas able to eat up to a third of their own body weight. An adult zebra can be consumed by 25 hyenas in a little more than 10 minutes. An interesting feeding adaptation of spotted hyaenas has been shown in the Serengeti ecosystem where several large carnivores are thought to be limited by the lack of mobility of their young and thus inability to follow migratory prey. Hyaenas counteract this by using a commuting system, described in detail by Hofer and East (Hofer & East 1993c), (Hofer & East 1993b) and (Hofer & East 1993a) whereby denning females can travel over 3500 km per year, returning from trips to feed her cubs (Hofer & East 1995).

Reproductive ecology

Female sexual maturation in spotted hyenas is around 3 years, whilst males become sexually mature slightly earlier. There is no clearly defined breeding season and gestation is between 98-132 days with an average litter size between one and four, averaging two. Birth occurs in a separate den and although the young are precocious they develop rapidly, starting to eat meat at 2.5 months, although weaning may take up to a year. Hyaenas usually begin hunting on their own when about 1.5 years old (Kruuk, 1972).

Conservation status

Spotted hyaenas appear to thrive in some areas with high human populations. For example, in Harar, Ethiopia, large numbers are actively encouraged by people feeding them (Kruuk 1972). In others areas hyaenas associate themselves with human settlements, especially pastoralists, feeding off scraps of skin, bones and cloth. In some cases human-derived resources can form an important part of the diet, for instance one of the Ngorongoro clans within the vicinity of a Maasai boma of Kruuk's (1972) study showed 59% of scats to contain livestock products. In another case, Serengeti hyaenas in the dry season were found frequently to visit a single boma and 96% of their scats contained livestock products. Such relationships with the Maasai may have been encouraged by the custom of placing the dead outside the boma (Kruuk 1972). However, the relationship with humans is generally negative and when human densities rise, hyaenas are generally exterminated (Kruuk 1972) (*e.g.* see "Attacks on livestock", p.25 and "Attacks on people" p.26). Apart from practical problems, hyaenas also tend to have an unpopular image (Kruuk 1972), (Frank 1998) similar to other dog-like species such as wolves *e.g.* (Kellert *et al.* 1996), (Breitenmoser 1998), (although see (Pate *et al.* 1996)) and wild dogs (Rasmussen 1999). Often portrayals of hyaenas in literature are poor, for example in Maasai literature the hyaena is always portrayed as a gluttonous fool (Kipury 1993) and in a study in Kenya, hyaenas were shown to be disliked in great disproportion to the relative damage they caused when compared to cats (Frank 1998). As a result they are hunted by Maasai herdsmen, shot by poachers who lose snared animals to them and were even reported to be still shot on sight in game controlled areas in the late 1960s (Kruuk 1972). Consequently, hyaenas have one of the greatest fleeing distances when humans are sighted, often over 300m (Kruuk 1972), *pers. obs.* Furthermore, many hyaenas are also lost through indirect human activities, with by-catch from snaring in the Serengeti ecosystem thought to remove approximately 8% of breeding females per year (Hofer & East 1995).

1.5 The Maasai

History and description of the Maasai

Of all the pastoralist groups the Maasai are some of the closest to “pure” pastoralists (Brown 1971). Maasailand was at its peak in the 1880s, after which it underwent a dramatic decline due to the effects of a rinderpest epidemic and has since been worn down further by international borders, colonial administration and the influx of large-scale agriculture (Homewood 1995). In present times, Maasai mainly inhabit Maasailand, a region straddling the borders of Kenya and Tanzania.

Social organisation and seasonal cycle

One of the features of Maasai culture has been a strong sense of identity (Parkipuny 1997). Consequently, the influence of other cultures has been relatively small and many Maasai still live traditionally. Indeed, it has been shown that the Maasai have gone to great lengths to work around the various impositions of legislation that might change their way of life in order to continue as they were *e.g.* (Homewood 1995). Although variations occur, the highest level of social organisation of Maasai society is the section, a loosely defined division often based around physical barriers (Spencer 1993). However, an alternative form of division is the clan, inherited through the paternal line. Clans are not divided into physical regions but are often centred around certain areas. Locally, the male Maasai are divided into age-sets: herdboys (children), *murran* ("warrior" class) and elders, with further subdivisions within each category (Homewood & Rodgers 1991; Spencer 1988). Herdboys are generally in charge of accompanying grazing cattle during the day. The *murran* are exempt from herding duties, apart from helping with particularly demanding tasks. Their official role is to fulfil the guarding role within the community, which includes retribution for cattle rustling by other Maasai or tribes as well as cattle raiding themselves. In addition, they enjoy a highly social time, filled with shows of bravery, such as lion hunts and long lasting bonds are formed. Recently a new division has been imposed. Following the *ujuma* or "villagisation" process of the 1970s, Maasai bomas have been organised into conventional villages often loosely centred on a school, cattle dip or similar service (Homewood & Rodgers 1991). This social structure has a strong influence on the Maasai interaction with the environment (Parkipuny 1997). The section and clan structures allow a level of communal land ownership and management, with the experiences learnt from herdboy to elder giving every man a rich knowledge of his region, the grazing areas and water sources. Furthermore, the close bonds formed during the *murran* period often form the basis for site choice and long-term mutual reciprocation while its democratic structure is continued to determine grazing rights and decisions (Homewood & Rodgers 1991).

In most cases, Maasai still live in an *nkang* or boma, a roughly circular communal living place for people and their livestock with a protective thorn fence around the outside, individual huts for people and a central *kraal* for animals. Most are clustered in villages but temporary bomas also exist in wet season grazing areas. Each boma will contain at least one (but usually several) family groups or *olmarei*, with the *olmarei* consisting of one elder man, his wife or wives and their children. Each *olmarei* will have a single gate in the boma through which people and livestock will enter. Often different *olmarei* in the same boma will consist of brothers or age-mates, but this can vary and composition is flexible (Homewood & Rodgers 1991).

Figure 2 – Inside a Maasai enkang. The hut is made of wood and cow dung and has only tiny openings to let light in and smoke out. In general a fire burns continuously inside. Calves are kept inside, cattle in a corral next to the hut. The outer thorn fence enclosing the corral and several huts can be seen in the background.

In conjunction with spatial differences, male Maasai are also divided into a series of age sets lasting approximately fifteen years, with women associated with an age set to a certain degree. Age sets are initially divided into two *elmurrata* before being joined in adulthood and given an *olporor* name (Spencer 1993). All members of an age set form a close relationship, beginning with a period of murranhood when men form a "warrior" class.

One of the essential features of the Maasai is that, like most pastoralists, they are transhumant (Homewood & Rodgers 1991), (Parkipuny 1997), (Spencer 1988), with their movements based upon such factors as the availability of water and grazing areas and avoidance of calving wildebeest and cattle-raiding risk areas (Homewood & Rodgers 1991). Although most have a relatively permanent boma in their home region dry season grazing area, most Maasai also use temporary bomas in the wet season where their cattle flourish and calve (Homewood & Rodgers 1991).

The potential importance of Maasai buffer zones for the Serengeti carnivores

Implications of source-sink dynamics for the Serengeti cheetah population

The levels of mortality found in the Serengeti plains cheetah population are so high that it has been suggested that the population is unable to sustain itself (Laurenson 1995b). This is supported by demographic modelling (Kelly 1998), (Kelly & Durant

In press). Based on 25 years of demographic data, it has been shown that the lifetime reproductive success of the Serengeti cheetahs has declined from the 1970s when it was a self-sustaining 2.1 cubs per lifetime to the 1990s when an unsustainable average of 1.6 cubs per lifetime were being produced (Kelly 1998). Since a self-sustaining population requires an average of two cubs per female per lifetime, it has been suggested that the plains sub-population is only able to persist due to immigration from a population outside the study area (Kelly 1998). Therefore in recent years the plains population fits the definition of a sink population, suggesting that there is a population outside the plans acting as a source.

Potential role of Maasai buffer zones

Modelling has suggested that relatively small increases in juvenile survival rates could have major effects on population outlook [(Kelly & Durant In press). Two strong candidates exist for the location of a population that might show the elevated survival prospects required for a viable population that could act as a source to the plains cheetahs. The Serengeti plains cover the eastern sixth of the Serengeti National Park. These are bordered by woodland to the west, which covers two thirds of the park (Sinclair & Norton-Griffiths 1979), and the multiple use areas of the Loliondo Game Controlled Area and Ngorongoro Conservation Area to the north east and east to south east. One hypothesis suggests that the increased cover in a woodland habitat could lower the impact of lions and hyaenas on cheetah cub survival, and the other suggests that human presence in the buffer zones may temper the effects of the larger predators to the benefit of the potentially less harmful cheetahs through increased cub survival (Laurenson 1995b). However, it has also been found that changes in adult mortality are potentially highly important for population viability due to the high reproductive value of adult cheetahs and their rapid breeding following cub loss (Crooks *et al*. 1998), therefore the benefits for cub survival would have to outweigh any impacts of hunting or poaching of adult cheetahs. Since the buffer zones north east and east of the Serengeti plains are inhabited by the Maasai, who have already been shown to likely have a negligible impact through hunting, these areas show high potential for holding source populations of cheetahs.

Chapter 2: Aims, study sites and general methods

2.1 Summary

In this section, the aims and objectives of the project are presented, based on questions raised in the introduction. The structure of the thesis is then described and the chosen study sites introduced. The second part of this chapter broadly describes the methods used for the study, the daily work protocols and some of the common analysis techniques employed throughout the thesis. In most cases, more detailed information for relevant methods is given in the relevant chapters.

2.2 Project aims

In chapter 1 the great importance of semi-protected landscapes was stressed, yet the conflicts that occurred between humans and wildlife within these areas can be highly detrimental to both sides constituting one of the major obstacles to their success. It is therefore vital to understand when, where and how successful coexistence between humans and wildlife at any level occurs so that conditions can be manipulated to encourage it. However, such issues need to be condensed into manageable portions. Therefore, in this project the aim was to add to this growing field of research by examining the ecological relationship between two specific representatives at either end of the spectrum of the human-wildlife conflict in semi-protected areas. On one side, large carnivores were taken to represent conflict at its worst, with many species threatened on a global scale primarily due to human activities whilst many humans risk attacks to their person or livelihoods if they live near them. On the other side, pastoralists, specifically the Maasai, were examined for their potential role in Serengeti carnivore ecology, representing a way of life that is practised all around the world that shows great potential for coexistence. If any coexistence with large carnivores can be found and understood there is great potential for coexistence with other taxa, and if any group of people are likely to display such characteristics, existing literature suggests it might be the Maasai.

In order to achieve this, four questions were asked:

1. Is carnivore prey availability reduced in the presence of people and livestock?

2. Are large carnivore populations reduced in the presence of people and livestock, and are the effects equivalent for all species?
3. Does the presence of people and livestock effect the behaviour of any large carnivores that do survive in these areas and are these effects the same for all species?
4. What role do the Maasai play in carnivore ecology outside the park? Do they have a highly detrimental impact on carnivore success or does their behaviour promote coexistence?

2.3 Thesis structure

In answering these questions, the thesis has been divided into eight main chapters, broadly outlined below:

1. **Introduction.** The first section introduced the current protected area system, including the concept of semi protected areas, buffer zones, and the reasons for their importance. The human-wildlife conflicts occurring in these areas were discussed and the specific cases of large carnivores and Maasai pastoralists were introduced.
2. **Aims and objectives, study sites and general methods.** In this section, the aims of the project are set out and the study site introduced, describing the varying levels of protection in the Serengeti ecosystem. An overview of the methods and analyses used in the study is presented.
3. **The potential prey base for large carnivores inside and outside the National Park.** In the study site description it is made clear that habitat availability is high in the semi-protected study sites. In this section the potential for carnivore success is explored further by examining the first hypothesis, comparing prey availability outside the park with levels inside and discussing the likelihood that Maasai activities are affecting carnivore ecology through prey depletion.
4. **Variation in large carnivore abundance with protection status.** Having explored the environmental factors required for carnivore success, the second hypothesis is tested by employing two techniques to measure abundance of each of the major large carnivore species inside and outside the park.
5. **An evaluation of methods used to survey large carnivores in semi-protected areas.** A wide range of literature exists on carnivore surveying and several

methods were used in this study. Since conditions outside core-protected areas can differ quite markedly from inside it was suspected that the choice of method could substantially affect the results produced. This section therefore does not examine any of the main hypotheses itself, but places the results from chapter 4 in context and makes recommendations for future work in semi-protected areas.

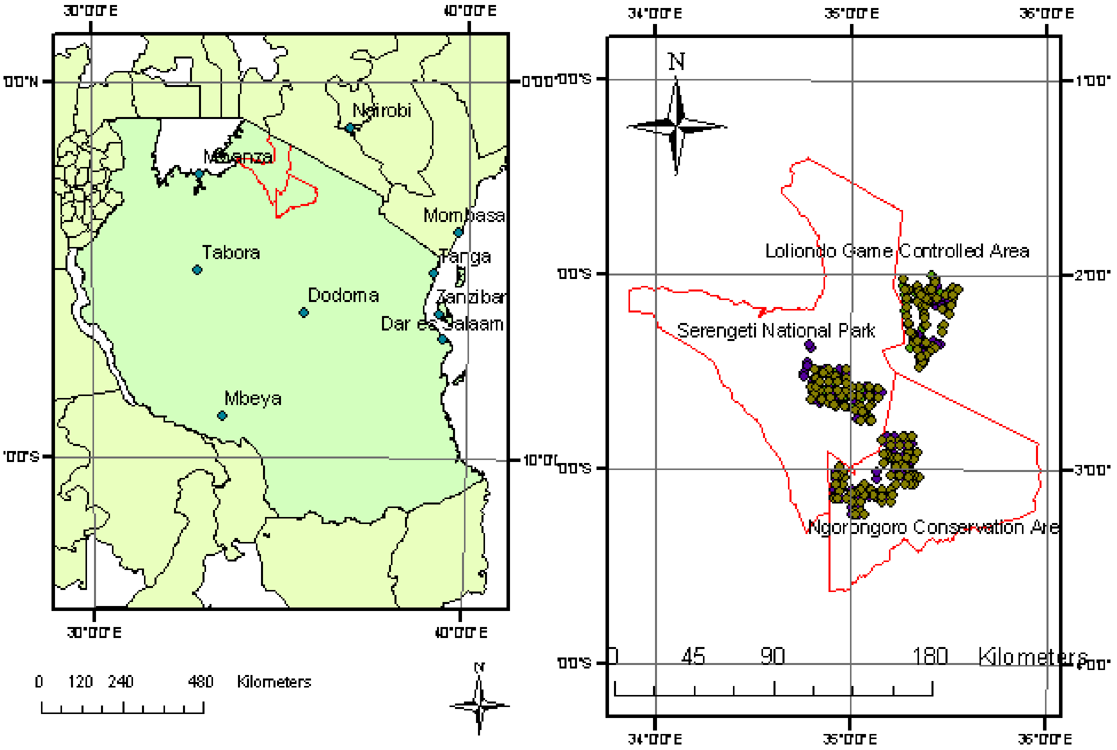
6. **Effects of protection on aspects of large carnivore behaviour.** The fourth section tests the third hypothesis by examining the carnivore populations described inside and outside the park in chapters 4 and 5 and determining whether they vary behaviourally, comparing measurements of activity, vigilance, responses to human stimuli and some aspects of hunting behaviour.
7. **The role of the Maasai in carnivore ecology.** The final data section tests the fourth hypothesis, examining Maasai attitudes to large carnivores as well as actual incidents of conflict. Levels of persecution are measured and any likely benefits to cheetahs at the expense of larger carnivores assessed.
8. **Discussion and conclusions.** The final section summarises the results from chapters 3-7 and assesses the current status of co-existence between large carnivores and Maasai. The relevance of the findings for carnivore and other wildlife conservation biology and human livelihoods both locally and globally are discussed and recommendations made for future work.

2.4 Study sites

Study site locations

The project was located in the Serengeti-Mara ecosystem or Serengeti Ecological Unit (Homewood & Rodgers 1991), an area defined by the route travelled by 3 million migratory species. The study was based in the Serengeti National Park, Tanzania (Figure 3), in a continuation of the cheetah research carried out there since the 1960s (first described by Frame and Frame (1981), continued by Caro (Caro 1994)) and comparing results from the park with two adjoining buffer zones. Both study sites located in buffer zones were placed in Maasai areas. These were chosen in preference to any other buffer zones to the National Park because, firstly, both appeared to be continuous with the National Park with very little obvious change in habitat (in contrast to some of the western boundaries where agricultural land extends up to the protected area borders). Secondly, they were chosen because both areas were occupied almost entirely by the Maasai tribe who live almost universally by a single lifestyle, thus simplifying any assessment of human influence. None of the protected area borders in the Serengeti ecosystem are divided with physical barriers allowing free movement of wildlife in all directions. The climate in this region is primarily driven by the Intertropical Convergence Zone (ITC) and to some extent the influence of Lake Victoria to the west. The ITC is an area of low pressure that moves seasonally over the equator, bringing a short rainy season between November and March (with an occasional break in January and February) and a wetter rainy season between March and May (Sinclair 1979). Due to a rain shadow caused by the crater highlands in the east, Serengeti rainfall occurs on an increasing gradient from the south east (seasonal means: 100mm dry, 400mm wet) to north west (seasonal means: 300mm dry, 800mm wet) (Sinclair 1979). Seasonal differences vary by region, a feature that drives the migration of some one million wildebeest as well as zebra and gazelles (Maddock 1979), (Durant *et al*. 1988). Two primary habitat types occur in the Serengeti ecosystem due to a hardpan of volcanic soils to the east, which is too thin to allow tree root systems. The southeast is therefore composed of the plains, an open grassland area interspersed with granite outcrops (“kopjes”) whilst the west and north, where soils are deeper, comprise open *Acacia* woodland (Sinclair 1979).

Figure 3 – Map of Tanzania, showing the position of the Serengeti, Loliondo and Ngorongoro protected areas (left) and a close up of the Serengeti region, showing the location of all study points (transects, call-is, scanning points) in each region



The Serengeti National Park

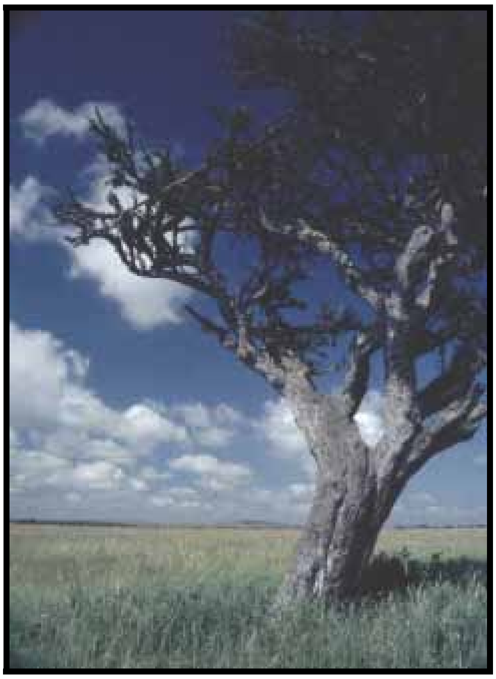
The control study site was 750 km^2 of the long grass plains (zone IV – 2 metre deep soil dominated by *Themeda triandra* and *Pennisetum mezianum* grasses (Sinclair 1979)) within the National Park where cheetah, lion and hyaena research was all being carried out simultaneously by other researchers and lying within the 2200km^2 study area demarcated by Caro (Caro 1994). Rainfall varies from approximately 100mm in the dry season to 5-600mm in the wet. The site was chosen primarily for its continuous habitat, avoiding any areas of grassland/woodland transition and to avoid areas of restricted access in the south of the park. Site size was maximised due to the large ranging habits of all of the large carnivores, but limited by the feasibility of covering it within approximately a week to allow time to visit other study sites within any given month. The Serengeti National Park is a core-protected area, patrolled by armed rangers. No humans other than those visiting or involved in the management of the park are allowed to live there (with most permanent buildings based at Seronera at the western edge of the plains) and none of the park resources are available for use by local people.

Figure 4 – The long grass Serengeti plains showing open grassland interspersed with granite kopjes.

The Loliondo Game Controlled Area

The first buffer zone study site was located in the Loliondo Game Controlled Area (Loliondo or LGCA). The LGCA is a region of 6734 km^2 lying to the north east of the park between latitudes 1°40'S and 2°50'S and longitudes 35 °10' E and 35°55'E with relatively low hunting pressure (Hofer *et al*. 1996) and reportedly similar proportions of woodland to plain habitat and rainfall levels to the Serengeti (Watson 1969). However, wet season rainfall can be slightly higher, up to a mean of 700mm (Sinclair 1979). It is an area that is used by both the main bodies of migratory animals, providing an estimated 2-3% of the resources consumed by the wildebeest and 2.5-3.5% of the resources used by zebras (Watson 1969), and also forms part of the range of separate populations of migratory wildebeest and zebra (Sinclair, *pers. comm.*) Within the LGCA the study area was centred on the most open grasslands in the region (known as "ang'atas" by the Maasai) in the south west which are continuous with the short grass plains in the Serengeti (Watson 1969). However, since no areas of continuous open grassland comparable to the Serengeti were available the study area was larger, 1250 km^2 to allow incorporation of the two largest ang'atas (Ang'ata Kheri and Ang'ata Nderi). Both of these areas were open habitat bordered by fine leafed *Acacia / Commiphora* woodland and interspersed with vegetated drainage lines or seasonal rivers. However, open areas were less well drained than soils in the park and therefore they also featured stands of stunted *Acacia drepanolobium* or "whistling thorn". As a game controlled area, Loliondo is protected to some degree and hunting without a license is illegal. However, the resources to enforce protection are not available and in practice, the area is effectively unprotected. In addition, Loliondo is home to the Maasai and Sonjo tribes, with the Sonjo restricted to a relatively small area in the east and Maasai vastly dominant. Settlements are primarily based around Loliondo town and to the West and South with no permanent settlements on the ang'atas. Almost all of the Maasai are agropastoralists, relying heavily on livestock, which is grazed on the ang'atas and in the forests, and to a lesser extent on subsistence agriculture. The LGCA also contains a concession to a professional hunting company, currently the Ortello Business Company, who hold the rights for hunting throughout the area. However, activities are mainly restricted to an area close to the park border in the north west of the region and at present use of the area is restricted to 2-3 months per year.

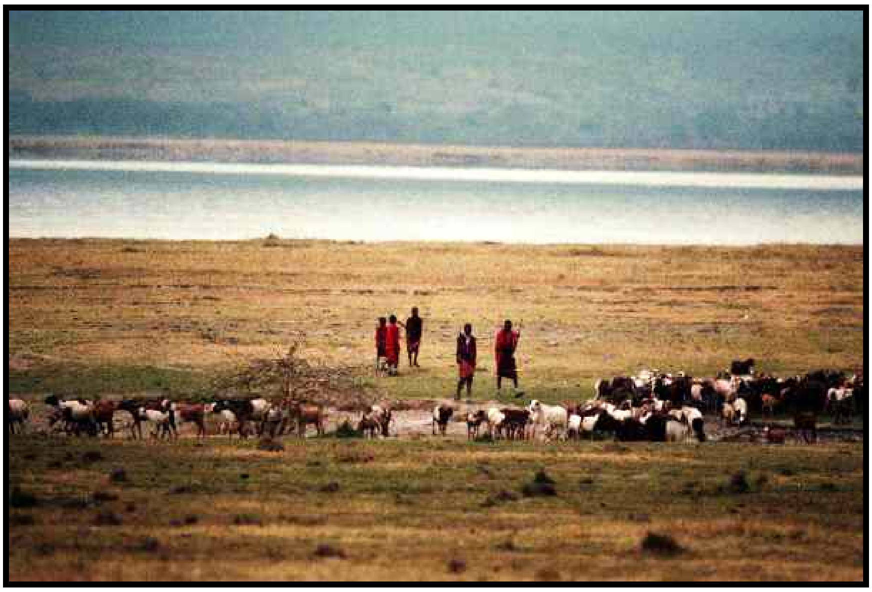
Figure 5 – A view over Ang'ata Kheri, Loliondo. Although dominated by large, open areas, Loliondo study area was interspersed with vegetated river gullies and stands of whistling thorn.



Ngorongoro Conservation Area

The second buffer zone study site was located in the Ngorongoro Conservation Area (Ngorongoro or NCA), directly to the east of the National Park. The NCA is an area of 8292 km^2 that was de-gazetted from the rest of the Serengeti National Park in 1959 by the Ngorongoro Conservation Area Ordinance as part of a deal removing the Maasai from the Serengeti National Park in return for guaranteed future rights in the NCA (Perkin 1995), (Shivji & Kapinga 1998) creating one of the first multiple land use areas in the world. However, human rights within the NCA were progressively eroded from the 1963 amendment act onwards, culminating in the banning of cultivation in 1975 and consequent decline in human welfare and nutritional status since (Homewood & Rodgers 1991), (Homewood 1992), (McCabe *et al*. 1992), (Shivji & Kapinga 1998) (also see Introduction). The NCA is now listed as a World Heritage Site, a Biosphere Reserve and contains archaeological remains at Olduvai and Laetoli dating back some 4 million years and comprises one of the most important tourist attractions in Tanzania (Homewood & Rodgers 1991), (Shivji & Kapinga 1998). Due to its location, much of the area lies in the driest area of the Serengeti ecosystem, with rainfall less than 100mm in the dry season and 4-500 in the wet (Sinclair 1979) Temperatures can reach 38 degrees in the Olduvai region (Homewood & Rodgers 1991). The study site covered 1200 km^2 to be comparable to the Loliondo site and was placed on the short grass “Serengeti plains” area (see (Homewood & Rodgers 1991) for further description) that is continuous with the plains in the east of the National Park. Habitat was primarily open grassland interspersed with granite kopjes, similar to the Serengeti site, with denser vegetation occurring around Olduvai Gorge, which bisected the area. However, since the hardpan layer to the east is closer to the surface, grasses in the study site were shorter than in the Serengeti, characterised by *Digitaria macroblephora* and *Sporobolus marginatus* species (for a more detailed vegetation description, see Herlocker & Dirschl, 1972). Within the NCA there were thought to be approximately 25000 Maasai in the late 1980s (Bureau of Statistics 1988). A count by Perkin (quoted in (Homewood & Rodgers 1991)) found 22637, although Shivji (Shivji & Kapinga 1998) claims 42,000 inhabit the area. It is now thought that approximately 22% of Tanzanian Maasai (approximately 100,000) live in the NCA (Homewood & Rodgers 1991). Two million migratory animals also use the NCA, generally arriving between December and April. Approximately 75% of the resources used by the migrants lie outside the Serengeti National Park and most of these are found in the NCA (Watson and Kerfoot, 1964, quoted in Homewood (1991).

Figure 6 – Short grass plains in Ngorongoro in the wet season. The plains are continuous with the short grass plains in the Serengeti and Loliondo protected areas.



2.5 Overview of methods

Daily work schedule

The work schedule was divided into three components. The first was based upon daily searching for predators, spending approximately one week per month in each study site, driving to predefined points and scanning the horizon with binoculars. Searching began at first light, generally around six a.m., and could continue until light faded around seven p.m. Usually a break was taken at midday. Some scan points were chosen for their visibility, located on hills or areas with unobstructed views. In the Serengeti, these were primarily based on existing scanning points used for cheetah research (S. Durant, *pers. comm.*). Outside the park these points were mapped during initial visits to the sites. These non-random scanning points maximised the chances of sighting predators in each region. However, in conjunction with these, random scanning points were also identified in each site, ensuring that cheetah sightings were not only limited to areas with high visibility. Random points were chosen using a random number generator and a map grid and each was visited every month. All scanning points were stored in a Garmin GPS. During this component of the fieldwork, all data on random predator sightings were recorded, including data on activity, all cheetah sightings were made for estimating population sizes, all cheetah behaviour was recorded, subjects for playbacks were identified and tested and continuous prey availability monitoring was carried out, although the latter data were not analysed in this project. When predators were sighted, sighting books were filled in, recording data required for a range of analyses (see appendix I).

The second component was also continuous and involved interviewing Maasai. This was only carried out outside the park. Following initial introductions to village chairmen, Maasai were interviewed at random, usually in the middle of the day to allow for some time for searching for predators in the morning. However, the distances involved driving from specific Maasai bomas to areas that needed searching were often inhibitory and interviewing became an all-day occupation. Interviews generally lasted a minimum of one hour, including time for general introductions and pleasantries.

The third component was repeated on a three-monthly cycle and involved large-scale surveys of scavenging large carnivores using call-ins and herbivores using line transects. Generally, call-ins were completed by nine o’ clock in the morning and the rest of the day was spent carrying out line transects, with a break during the hottest hours. Quarterly surveys of all three regions were very labour intensive and usually took at least one month to complete.

Data Collection Methods

Most data were collected using a Psion Organiser LZ64 for its advantages in speed of data entry, its ability to download straight into a computer and for the accuracy it allows for recording data in real time. Separate programs were written in the Psion OPL language for trip logging, all transects, call-ins and all behavioural observations and data were downloaded to a laptop computer, edited and backed up at the end of every day. Only predator sightings and questionnaires were recorded on paper due to the greater flexibility required for data entry. Details on each of the programs are included in the appendices.

Fieldwork timing

Following an initial 2 month training period inside the Serengeti National Park at the end of 1999, fieldwork was carried out in the Serengeti and Loliondo between April 1999 and May 2001. Ngorongoro was added to the study at a later point following difficulties with data collection in Loliondo and fieldwork undertaken between July

2000 and May 2002. Fieldwork was not completely continuous, with occasional gaps when working in the UK.

Analysis

When possible, data were analysed using parametric tests. Only when data were not normal, and could not be transformed, were non-parametric tests were used. In many cases analysis was carried out by fitting Generalised Linear Models (GLMs) to response variates using Genstat 5.3.2. GLMs have the advantage over other multivariate techniques of allowing specification of non-normal error structures and can correct for transformation (Crawley 1993). When GLMs were used the maximal model of biological meaningful parameters were initially fitted to the response variate. However, significantly correlated parameters were never added together since they would cause inaccurate estimations of variance (Russell *et al*., in press). Parameters and their interactions were then dropped sequentially in a step-wise reduction to determine their significance and the least significant term removed permanently from the model. This process was continued until the minimal model was reached when removal of further terms significantly ($P<0.01$ unless stated otherwise) reduced the explanatory power of the model (Crawley 1993).

In some cases Iterative Residual Maximum Likelihood Models (IRREML) were used. IRREMLs are similar to GLMs, allowing analysis of non-normal data. However, they also take account of random and non-random terms. Random terms allow factors that have been repeatedly sampled or pseudoreplicated to be incorporated into the model. The significance of IRREML terms were assessed by their Wald statistics (represented by χ^2) which approximately follow a chi-squared distribution.

The results presented for GLMs and IRREMLs show the significance of each parameter entered in the maximal model. Interactions are depicted by "*" For significant parameters this refers to their effect in the minimal model. For non-significant terms it shows their effect when added to the minimal model. The values for individual components of interaction terms were obtained by running models without the interactions. The average effects and standard errors for minimal model terms are also presented, showing whether the relationship with the response variate is positive or negative when setting the lowest value, (numerically or alphabetically) to zero. The significant model was then used to predict values for given parameters, controlling for all other factors in the minimal model. These results are generally presented graphically. Controlled factors were set at their mean value.

Chapter 3: The potential prey base for large carnivores inside and outside the Serengeti National Park

3.1 Summary

One of the most important prerequisites for carnivore survival is prey availability. Generally, prey populations are significantly reduced when sharing land with humans due to hunting pressure or resource competition and thus the potential for carnivore success is reduced. However, it has been argued that traditional pastoralists have a lower impact on their environment, which can be compatible with various herbivore populations. In this chapter, the prey populations are compared between the Serengeti National Park and its pastoralist-dominated buffer zones. Eight line transect surveys were conducted over two years covering 2087 kilometres and sufficient data were collected to compare densities of fifteen prey species. The results showed that prey levels inside the park were no higher than outside the park. Almost no difference was found in the diversity of species occurring inside and outside the park. Biomass, when measured as a two year average, was higher outside the park ($\chi^2_2 = 49$, $p < 0.001$) than inside. Differences remained significant when both migrant species and livestock were excluded from analysis. Biomass levels were comparable to previous surveys of the area, fluctuating around 4000kg/km^2. The only species consistently more common within the park were kongoni, topi and warthog. However, temporal variation was significant for every species, including non-migrants. Furthermore, temporal variation for each species was not consistent and varied inside and outside the park for all species except giraffe, eland and kongoni. It is therefore concluded that the mere presence of people and livestock within the environment does not reduce the prey availability for carnivores. Furthermore, the survey shows that snapshot comparisons of density are of little value. Instead, it is suggested that rather than trying to determine specific prey levels inside and outside the park it is more informative to see the area as a highly dynamic and variable system in which the buffer zones play an equally important role as the core-protected areas.

3.2 Introduction

The relevance of herbivore populations for carnivore studies

The importance of prey populations for carnivore ecology is undoubted, with many predator populations thought to be limited by prey availability (*e.g.* (Bertram 1975), (Brand & Keith 1979), (Fuller 1989)). However the exact relationship between predator densities, migratory prey and resident prey in the Serengeti ecosystem is still disputed. There is some evidence that, since predators cannot follow the migratory herds, either due to limits on foraging ranges or because of periods of restricted movement whilst raising young (Kruuk 1972), (Schaller 1972b) they must be regulated by non-migratory ungulate density (Fryxell & Sinclair 1988). Thus, when the migratory animals are in range there is a surplus of food but predator populations cannot increase to exploit this resource as it is only temporary. In fact, following the assumption that predators follow a Type III functional response, whereby they switch to the most common species in an area, it has been suggested that predation avoidance could be a factor driving the migration (Fryxell *et al.* 1988). The strong relationship between prey availability and predator populations is supported by Carbone and Gittleman who showed that a strong, linear relationship exists between prey availability and carnivore density (Carbone & Gittleman 2002). However, the strength of this relationship in the Serengeti has been questioned by Hofer and East (1995) who suggest that predator-prey relationships may be more complex, since cub mobility of most carnivores is only limited for two months whilst prey choice data do not support these hypotheses. They suggest that resident prey may still limit some predator populations, but through social factors limiting movement or hunting specialisations rather than cub mobility or ranging limits. Furthermore, they suggest spotted hyaenas show no limitation by resident ungulates due to the commuting system (Hofer & East 1993c) which allows them to follow the migration whilst leaving young at the den and therefore exceed the expected carrying capacity of a territory (Hofer & East 1995). This is supported by data from Ngorongoro Crater where hyaenas living with high densities of resident prey show no reproductive differences from hyaenas in a migratory-dominated system in the Serengeti (Hofer & East 1995). Historical data suggest that Serengeti spotted hyaenas may still be limited by overall prey densities, since populations have doubled and recruitment has risen from 5.2-9.9% during the great increase in migratory wildebeest between 1968 and 1986, but that human-caused mortality and siblicide were also important limiting factors (Hofer & East 1995). Equally, cheetahs appear to live at lower densities than might be expected from prey availability, probably because they themselves are regulated by predation by lions and hyaenas that cause high juvenile mortality (Laurenson 1995b).

Herbivore populations outside protected areas

Semi-protected areas form the majority of protected land in Africa (Caro 1999d). They hold huge numbers of herbivore species and the species that rely on them, provide vital seasonal habitat for animals theoretically protected by National Parks (*e.g.* see Borner, 1985, Mwalyosi, 1991, Norton-Griffiths, 1995) form the basis for much debating on the impact of humans on their environment (*e.g.* see Lamprey, 1983, Homewood, 1991) and are the site of much human-herbivore conflict in terms of crop raiding, competition and disease (*e.g.* Newmark *et al.*, 1994, Parkipuny, 1997). Despite this, herbivore studies are overwhelmingly focussed on National Parks or other fully protected areas (Caro 1999d). In one of the few studies of semi-protected areas, Caro (1999) compared a National Park with varying classes of buffer zones in the Katavi ecosystem of Tanzania. He showed that, controlling for habitat differences, large and medium herbivores were surviving outside the park with varying success. In a game controlled area shared with pastoralists and tourist hunters, mammal diversity and density were high. In a logged and resident-hunted area diversity and density were low and in an open access area supporting all land use types density was low but seasonably variable. No species were more common outside the park. This led to the conclusion that state-owned multiple use conservation areas could not be relied upon to conserve large and medium mammals without human removal or community conservation schemes (Caro 1999d).

The effect of humans on herbivore populations

Although few in depth studies have been conducted on the actual changes that occur within herbivore populations when humans are present, much debate centres on the potential mechanisms for impact. The main ways humans could potentially affect herbivore populations are through direct impacts (for example hunting or snaring) or indirect (for example habitat change due to land conversion or competition and habitat change through livestock). Direct impacts are not expected to be an issue for this study (see Introduction and Chapter 7) however, indirect impacts are frequently cited when discussing pastoralists and their environment. For example, in Loliondo it was shown that productivity was similar to the Serengeti, but that Maasai cattle largely replaced wildebeest as the dominant herbivore (Watson 1969). Similarly, in the Kalahari multivariate statistics were used to show distance to bore holes (used as an index of pastoralist presence) to be negative determinants of non-migratory species distribution (Verlinden 1997) and in a second study in the same area wild herbivore species were also significantly further from villages than livestock (Bergstrom & Skarpe 1999). Both studies showed ostrich, springbok, hartebeest and gemsbok to be the least tolerant. In many cases, the presence of an effect of pastoralists on wildlife is simply assumed to be damaging and recommendations are made to restrict human activities (*e.g.* Verlinden, 1997). However, the effects of pastoralism are not always as detrimental as generally assumed. For example, one long-term study compared wildlife declines either side of the Tanzania-Kenya border where political and economic forces varied but environmental variables did not (Homewood *et al*. 2001). The study showed sharp, long-term declines in almost all species since the mid-1970s on the Kenyan side, where communal land was being privatised into ranches, but not on the Tanzania side, either in the National Park or in the Maasai buffer zones where populations were fluctuating about a stable mean. This was supported by a study showing wildebeest declines of up to 81% in the northern Serengeti-Mara ecosystem which were originally attributed to competition with cattle around the reserve, but were shown to be more likely attributable to the loss of grazing lands to agricultural encroachment (Ottichilo *et al*. 2001). In a comprehensive study within Tanzania, Caro examined the effect of protection, human presence and activities on aerial census estimates of wildlife biomass. He showed that human presence *per se* reduced herbivore biomass (Caro *et al*. 1998a), but that the pastoralist-dominated Game Controlled Area still had relatively high biomass whilst logged areas with high resident hunting had greatly reduced herbivore biomass. The reasons for the differences were attributed primarily to hunting - partially tourist and resident hunting but primarily illegal hunting (Caro 1999d). Another example of direct impact comes from a later study in the Kalahari where Verlinden *et al* (1998) showed that springbok were not affected by human presence at all, that steenbok and duiker were possibly affected and that only gemsbok were much rarer near livestock than further away, and this was thought to be due to hunting pressure. Nevertheless, warnings of the damage pastoralism was causing were still made in the paper (Verlinden *et al*. 1998).

The exact effect of humans on herbivores in many circumstances therefore remains open for debate. In a final example, a study of 20 years of herbivore densities inside and outside the protected Mara reserve in Kenya by Ottichilo *et al* (2000) found that throughout the system, non-migratory herbivore densities had declined by 58% and up to 72% for some species. However, more individuals were found outside the park and no difference was found between declines or rates of decline inside and outside the park showing either that declines were not due to factors outside the reserve, or that these factors affected animals inside and outside the park equally (Ottichilo *et al*. 2000). Such findings suggest a need for further studies of herbivores and human relationships outside protected areas and to try and understand the interactions in terms of a wider, dynamic ecosystem approach.

Alternative theories in rangeland science

The debate over the indirect effect of humans on their environment though livestock use lies at the root of the central debate in rangeland science The two main schools of thought can be summarised as the “old” and the “new” paradigms (Warren 1995), although perhaps “dominant” and “alternative” paradigm would be more appropriate since the newer theory has by no means supplanted the older in many people’s understanding. The dominant view states that pastoralism often leads to overgrazing and environmental degradation due to overstocking above the carrying capacity of the land, thereby upsetting the equilibrium. This is a process driven by the Tragedy of the Commons (Hardin 1968) whereby rational individuals gain no benefit from restraint due to open access of the resource, and cultural practices that encourage irrational overstocking for prestige and wealth. Such a view is expressed in various forms by a wide range of authors (*e.g.* Brown, 1971, Coe *et al*., 1976, Lamprey, 1983, Sinclair & Fryxell, 1985, Mizutani, 1998, Letnic, 2000) to the extent it is so widely accepted that it forms the basis of many conservation and development programmes and is often presumed to occur without evidence to support it (Homewood & Rodgers 1991), (Homewood & Brockington 1999). However, this view has been challenged by a range of authors (*e.g.* Sandford, 1982, Ellis & Swift, 1988, Homewood, 1991, Behnke & Scoones, 1993, Homewood, 1994) who suggest that semi-arid rangeland systems do not exist at equilibrium and instead show chaotic shifts between multiple alternative states, driven more by abiotic factors, such as rainfall, than overgrazing. The concept of a single carrying capacity is therefore seen as irrelevant over any significant length of time and apparent degradation may simply be the product of a fluctuation dip. Furthermore, nomadic pastoralism, based on land use decisions that may appear irrational to the western eye, is the most efficient system to exploit such conditions (*e.g.* Homewood, 1991, Homewood, 1994).

Herbivores in the Serengeti ecosystem

One of the best surveyed areas in Africa is the Serengeti ecosystem, with one of the earliest attempts at surveying the National Park carried out in the 1950s by Pearsall (Pearsall 1957). The need for long-term censusing over large areas was realised by Sinclair and the first of subsequent regular large scale census of resident herbivores was carried out using aircraft-based strip sampling in July 1971 (Sinclair 1972) with a follow up in August 1976 (Grimsdell 1979). Until this point very little surveying had been carried out beyond the park boundaries, with the exception of one survey in the Loliondo Game Controlled Area in the late 1960s using a mixture of aircraft total counts and strip transect sampling (Watson 1969). Migratory animals were not included in the census, although it was estimated that the LGCA provided 2-3% of the resources required by the migratory wildebeest and 2.5-3.5% of the resources for migratory zebra when they used the south western plains contiguous with those inside the park (Watson 1969). Surveys carried out from the 1980s by the Serengeti Ecological Monitoring Programme included both an increased area within the Park and included areas within the surrounding lands. A summary of population censuses to determine densities and trends inside and outside the park has been produced by Campbell and Borner, covering aerial surveys from the 1960s to 1991 including the National Park, and parts of the Ngorongoro Conservation Area, Maswa Game Reserve and Loliondo, Ikorongo and Grumeti Game Controlled Areas (Campbell & Borner 1995). It showed all species appeared to be more successful inside the park, with the exception of roan that was absent from the park but existed in extremely low densities near human populations in the Maswa GR where it is thought human influence lowered competition by other ungulates. Some areas to the north west of the park (Ikorongo and Grumeti GCAs) and western Maswa GR suffered very low densities (<1 individual per km^2) of resident herbivores. However, the Loliondo GCA, Maswa/Makao border and a small region near the Ikoma gate showed wildlife distributions at a significant distance from the park boundary. Loliondo populations were not reported to have changed appreciably since Watson's survey and, in the case of giraffe, had increased (Campbell & Borner 1995). Censuses specific to the Ngorongoro Conservation Area have been carried in 1980 by EcoSystems and in conjunction with the Ngorongoro Conservation and Development Project but again methodological differences have hampered comparisons (see Perkin 1995 for a summary).

Chapter aims

In order to examine the differences between carnivore prey populations inside and outside the park, five questions were investigated:

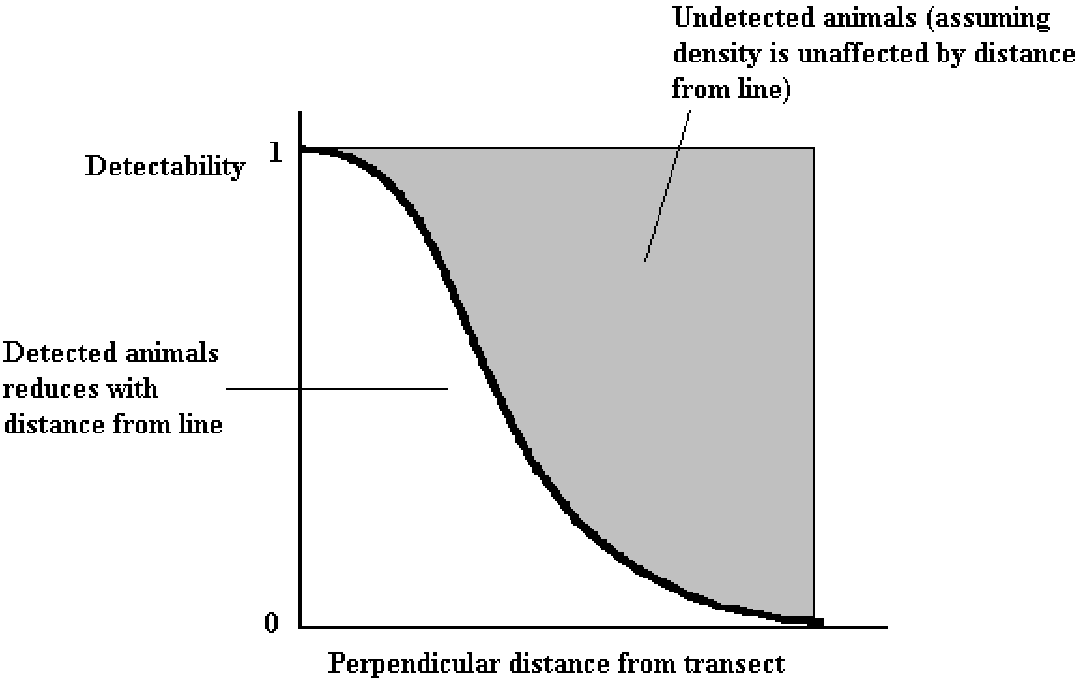
1. Is species richness different outside the park from inside – are there any species from the Serengeti not found in the semi-protected areas?
2. Is species abundance different outside the park?
3. Is the temporal fluctuation equivalent outside the park?
4. Do the differences between the Park and semi-protected areas support research that suggests humans have a negative effect on ungulates in semi-protected areas?
5. What are the likely implications for carnivores outside protected areas?

3.3 Methods

Introduction to transect surveying

A group of methods commonly used for estimating wildlife density and abundance are quadrat-based methods, such as strip transects or point transects, whereby all individuals within a set distance from a transect line or point are counted and densities estimated by dividing the total count by the area surveyed (*e.g.* see Caro, 1999a or Bergstrom & Skarpe, 1999). However, such methods assume that all individuals within the surveyed area are recorded, an assumption rarely met and impossible to test using the survey data (Thomas *et al*. 2002). Furthermore, such methods are wasteful since to increase the probability of recording all individuals the surveyed area has to be very small, thereby discarding up to 60-80% of observations (Anderson *et al*. 2001). An extension of quadrat-based methods are line and point transects in which the perpendicular distance to the sighting is recorded (Buckland *et al*. 1993). Assuming that objects are spaced randomly with respect to the transect and that detection probability at distance 0 is 100%, the increasing number of missed sightings with increasing distance can be modelled using a detection function and thus the proportion of missed sightings estimated (see Figure 7)

Figure 7 – Distance theory (adapted from Buckland *et al*, 1993). The curve shows the fall off in detectability of sightings as they are further from the line. By determining the particular curve for a given species or habitat (the detection function), the number of sightings missed can be calculated.

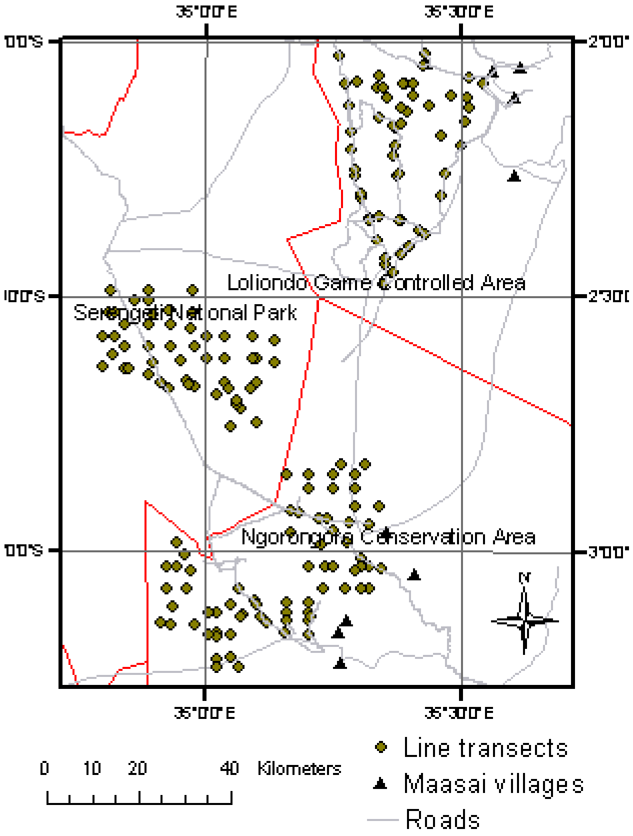


For this survey, line and strip transects were used to estimate herbivore densities. Line transects are the method most commonly used distance-based method for surveying the larger mammals in preference to point transects (*e.g.* African ungulates and livestock (Caro 1999b), (Mizutani 1998), deer (White *et al.* 1989), foxes (Heydon *et al.* 2000), wallabies (le Mar *et al.* 2001), gorillas (Remis 2000) or squirrels (Hein 1997)). This is probably because they are more efficient (most travelling time is spent collecting data) and because relatively more sightings are made nearer the line, which are the most valuable area for density estimates, than for point transects where the area close to the point is small but very large at further distances (Buckland *et al.* 1993).

Transect placement

Analysis of transects requires that the transect routes are placed randomly with respect to the objects counted (Buckland *et al.* 1993). However, a completely random placement of line transects during a pilot run resulted in transects crossing rivers, rocks and other problematic or sometimes impossible terrain. The consequent time demand of each transect and wear on the vehicle meant that a completely random placement was too inefficient. Therefore, transects were placed randomly when possible but each region also included several transects on “roads” (all weather dirt tracks) and “tracks” (smaller, lesser-used tracks generally impassable in wet conditions). The road type for each transect was recorded to allow a comparison of any differences. Almost all transects were precisely five kilometres long.

Figure 8 – Position of line transects in the study areas. Each point represents the start or end of a transect. Red lines show the protected area borders.



Transect protocol

Line transects

Transects were carried out by a single observer driving below 20 kph in a Land Rover, scanning in both directions and along the transect line scanning without binoculars and recording all mammals larger than a mongoose and ostriches (a known prey item for lions (Schaller, 1972b)). The majority of transects were not carried out at the hottest point of the day in case animal grouping or distribution was affected (for example by animals clustering under the shade of trees). Sightings were recorded by group, since individuals were not independently distributed, defining a group as an animal(s) at least 100 metres from its nearest neighbour. Distance measurements were made to the perceived geometric group centre and for almost all cases, estimates were delayed until the object was perpendicular to the car. In cases where objects ran from the car the point at which they were first observed was fixed upon and again the perpendicular distance estimated by eye once the car was level. Such flushing occurred surprisingly rarely and when it did, animals were usually very close to the line allowing for fairly confident distance estimates. Precise distance estimates are essential for analysis. Therefore, a Bushnell laser range finder was used, which was effective for up to 300m. Further distances were estimated by eye and regular checking was carried out whilst driving by estimating the distance to an object ahead and checking accuracy with the vehicle odometer. Distances were recorded to the nearest metre. Although such accuracy at further distances was highly unlikely, it is preferable to collect data as accurately as possible in the field and to group into appropriate intervals at the analysis stage (Buckland *et al*. 1993).

In addition to distance, group size, species and various environmental parameters (see

Table 4) were also recorded for each sighting. Ideally, number of individuals in the group should be recorded equally accurately for all distances. Therefore, binoculars were used to confirm group sizes at larger distances. However, it is assumed that distance will have some confounding effect on group size estimation (Buckland *et al*. 1993) and this is incorporated into the analysis. Transect length was measured using the vehicle odometer.

Table 4 – Data recorded for each transect sighting

Factor	Notes
Study area	Loliondo / Ngorongoro / Serengeti
Transect number	A unique code for each transect
Odometer reading	Between 0 and 5000
Perpendicular distance to group centre	Distances were initially estimated by eye and in later surveys using a range finder. Distances by eye were practised whilst driving, estimating the distance to an object ahead and comparing with the odometer. Exact distances were recorded rather than distance categories. Group centres were estimated by eye.
Group size	For mixed herds, overall group size and composition was recorded as well as the number of each given species. Animals were deemed to be within the same group if they were within 100m of one another.
Species	All mammals larger than a mongoose were recorded
Time	Time of day
Habitat	Recorded every 1000m and for every sighting
Road type	Off-road / track / road
Temperature	Recorded for later surveys only

High density transects

When migratory wildebeest and zebra passed through the study areas, and to some extent Thomson's gazelles, the density of animals increased to such an extent that the requirements for distance sampling from a car were not met since animals formed giant herds with no discernible centre for measuring distance or edges for determining group size. In many cases a continuous spread of animals could be seen stretching to the horizon in several directions. In these situations, transects were surveyed as a strip transects (Buckland *et al*. 1993) with a half width of 200m, recording the total number of every species occurring within the strip. Strip width choice is a balance of precision (increased by a larger sample area) and bias (reduced with smaller strip widths where 100% detection is more likely) (le Mar *et al*. 2001). Therefore 200 metres was chosen as the largest distance within which 100% detection was likely since the high densities tended to occur in the open habitats where visibility was excellent. A Psion computer was used to record individuals, with every sighting requiring a single key press to record in an effort to make the counting of large numbers more efficient. Since line transects account for differentiation in detectability as well as number of sightings they are a more accurate survey tool (see Buckland *et al*, 1993 and le Mar *et al*., 2001). Therefore whenever a line transect was possible it was carried out. Only if individual groups could not be discerned and a line transect was impossible would a strip transect be used.

Census timing

Line transect surveys were carried out in conjunction with call-in surveys (see Chapter 4). The first survey was carried out in July 1999 in the Serengeti and Loliondo and subsequent surveys were carried out every 3 months until April 2001 giving a total of eight surveys across two years. The same transect routes were used for every census to remove the effect of local spatial conditions on density and increase the statistical power for detecting trends across time (Buckland *et al.* 1993). To enable accurate repetition, transect start and end points were recorded to the nearest 10 metres using a Global Positioning System and off-road transects were driven in as close to a straight line between the two points, whilst road transects simply followed the road. Surveys in Ngorongoro were only started in July 2000 giving a total of four surveys across one year. A complete survey of all three study areas typically took approximately one month.

Analysis

Density estimation

Transects were analysed using distance theory (Buckland *et al.* 1993) and the DISTANCE computer program (Laake *et al.* 1998). Habitat type was recorded at 100m intervals for line transects and only transects located in predominantly open grassland habitat were included in the analysis. Data were analysed using groups (herds) as observations rather than individuals, since individuals were not spaced independently of one another (Buckland *et al.* 1993). Because detection functions can vary significantly between species (le Mar *et al.* 2001) separate detection functions were fitted to each species with sufficient sightings. Histograms of sightings plotted against distance were used to initially examine the data for evidence of heaping (a human error resulting from a tendency to allocate distances to common intervals such as 50 or 100m as opposed to 49m or 103m) and to check for any evasive movement away from the line (seen as a peak at a distance above 0) which would both affect density estimates. Data were then grouped into suitable intervals (at least five intervals were used so as not to affect the power of the test too greatly (White *et al*. 1989) and truncated to ensure a reasonable fit to the shape criterion specified by DISTANCE (Buckland *et al*. 1993). The most appropriate intervals and truncation were selected for each species individually. Detection functions were then fitted for each species, pooling data across transects and time since there was no reason to believe detectability would vary with time. Models were built from all combinations of four key functions offered by DISTANCE (uniform, half normal, hazard rate, negative exponential) and three series expansion functions (cosine, simple polynomial, hermite polynomial). Each of these key functions fit the desired robustness, shape criterion and estimator efficiency required of models fitting distance data, with the uniform function having no parameters, the half-normal a single parameter estimated from the data and the hazard rate requiring two parameters from the data (Buckland *et al*. 1993). Expansion terms could then be used to adjust the models by adding one or two parameters to improve the fit, although key functions alone were usually sufficient. Akaike's Information Criterion (AIC) was used to select the most appropriate key function whilst adjustment terms were added sequentially and the best chosen using a Likelihood Ratio Test. The match of the best model to the data was assessed using a Chi-squared goodness-of-fit (GOF) test using $P<0.15$ as a cut-off point (Buckland *et al*. 1993). Post stratification was then carried out by transect to give a density of groups for each species for each transect.

To calculate densities of individuals, average group size was required. However, taking a simple mean often over-estimates group size due to the higher likelihood of detecting larger groups with increasing distance, therefore log group size was first regressed against log detection probability (Buckland *et al*. 1993). If the regression was significant at the $P=0.15$ level (recommended by Buckland *et al*, 1993), the predicted group size estimate adjusted for distance from the regression was used; if the regression was not significant, or insufficient data available for a regression, the mean was used. Average group size was estimated for each transect to account for any variation in grouping spatially or temporally.

Strip transect data were also analysed by species using DISTANCE software by fitting a uniform detection function to the data, with a sighting distance to every animal specified as the strip half width (200m). Sightings were analysed by individual rather than group since individual herds could not be determined.

Distance analysis requires fairly large sample sizes to obtain accurate detection functions and average group size estimations, with 60-80 sightings the recommended minimum (Buckland *et al*. 1993). For most species data were sufficient, but some of the scarcer species have large variance in the estimate whilst the rarest species could not be analysed using DISTANCE.

Determinants of density

Generalised Linear Models (GLMs – see Methods chapter) were used to investigate differences between study regions across time whilst controlling for any other potentially explanatory variables. Each variable was added to the GLM as a separate model term (see Table 5)

Table 5 – Potential explanatory variables used in the Generalised Linear Models

Model term	Levels
Region	Serengeti, Ngorongoro or Loliondo
Year	1 or 2
Season	Dry start (July), Dry end (October), Short wet (January), Long wet (April)
Time of day	Time transect was started (early – before 10; mid – 10-3; late – after 3)
Road type	On or off-road
Region * Month	Interaction between region and season
Region * Year	Interaction between region and year
Year * Month	Interaction between year and season
Region * Road type	Interaction between region and road

A GLM with Poisson-distributed errors was fitted due to the high number of zero observations and the appropriate log link function (Crawley 1993). All terms were fitted to the response variate (density, measured as individuals per square kilometre) in the maximal model and a stepwise reduction used to remove non-significant terms. The results presented show the significance of all terms and the effects and standard errors of the minimal model components. When quoting significance this refers to significance within the minimal model for significant terms and the result of addition to the minimal model for non-significant terms. The values for individual components of the interactions show their significance when no interactions were added to the model.

Survey effort

A total of 2087 km of line and strip transects were conducted in open grassland habitats in the three study sites across two years. Survey effort was not equal throughout the study since the Ngorongoro study area was not added to the census until July 2000 and variation occurred between surveys due to time limitations or driving conditions (Table 6). Strip transects were only used rarely (Table 7). About 61% of transects were carried out off-road, distributed randomly. Loliondo was the most restrictive habitat with only 52% of transects off-road. The Serengeti could potentially have been completely off-road but 40% of transects were conducted from roads to allow the effect of roads on density estimates to be determined (Table 8).

Table 6 – Summary of survey effort for all grassland transects. Effort was greater inside the Serengeti since several transects outside the park were discarded if they did not pass through predominantly grassland habitat.

			Region		
Year	Season	Data	Loliondo	Ngorongoro	Serengeti
1 (July 99-May 00)	Dry start (July)	No. transects	4	0	22
		Sum of transect length	20	0	134
	Dry end (Oct)	No. transects	10	0	28
		Sum of transect length	50	0	140
	Short wet (Jan)	No. transects	12	0	25
		Sum of transect length	60	0	123
	Long wet (Apr)	No. transects	10	0	27
		Sum of transect length	50	0	135
2 (July 00 – May 01)	Dry start (July)	No. transects	14	28	30
		Sum of transect length	70	140	150
	Dry end (Oct)	No. transects	14	25	30
		Sum of transect length	70	125	150
	Short wet (Jan)	No. transects	13	25	30
		Sum of transect length	65	125	150
	Long wet (Apr)	No. transects	14	25	27
		Sum of transect length	70	125	135
Total no. transects			91	103	219
Total distance (km)			455	515	1117

Table 7 – Summary of transect types used. Due to the increased accuracy of line transects, strip transects were only applied when line transects were not possible.

		Region		
Transect type	Data	Loliondo	Ngorongoro	Serengeti
Line	No. transects	81	75	214
	Sum of transect length	405	375	1092
Strip	No. transects	10	28	5
	Sum of transect length	50	140	25

Table 8 – Summary of transect effort on and off roads[1].

		Region		
Road type	Data	Loliondo	Ngorongoro	Serengeti
Off road	No. transects	47	76	128
	Sum of transect length	235	380	664
	% total	52	74	59
On road	No. transects	44	27	91
	Sum of transect length	220	135	452.7
	% total	48	26	41

[1] Off-road transects were always preferred since they could be randomly placed but terrain forced use of roads in some areas. In the Serengeti where off-road driving was always possible, some road transects were included for comparison.

3.4 Results

Species diversity

Twenty one species considered potential carnivore prey were recorded during the transect census (Table 9). Of these, twelve were sighted sufficiently frequently to estimate detection curves for Distance analysis. Not including livestock, fifteen of the species were seen in Loliondo, fourteen in Ngorongoro and fifteen in the Serengeti. Differences in species richness were negligible and attributable to differences in the surrounding habitat of the areas surveyed. No species was commonly seen in one area but absent in another. Several species were more usually associated with wooded habitats but occasionally moved into fringe areas. Of these, elephants were not sighted on grasslands outside the park during transects, but were sighted at other times and in other habitats in Loliondo and Ngorongoro. Buffalo were also seen in all areas but not during transects. Impala are also a woodland species that occasionally moved into open areas bordering woodlands in Loliondo. Reedbuck and waterbuck were not seen outside the park but both have strong reliance on permanent water sources, which were available just outside one part of the National Park study site. Mountain reedbucks were only sighted in Loliondo but not during transects. Again these were associated with a specific habitat type (rocks). The smaller antelopes seen in Loliondo are generally associated with bushy habitats and were spotted when passing through bushy patches at the edge of the open areas. No people or livestock were recorded inside the park (expectedly since they are actively excluded by law). A full list of the entire range of species seen on transects is included in the appendix (p. 354).

Table 9 – Summary of all large herbivore or potential carnivore prey sightings of groups / total number of individuals recorded on grassland transects between July 1999 and April 2001. Species with sufficient sightings for analysis with DISTANCE are highlighted.

		Loliondo	Ngorongoro	Serengeti	Total
Buffalo (*Synceros caffer*)	Sightings	0	1	1	2
	Individuals	0	70	5	75
Cattle (*Bos indicus*)	**Sightings**	**72**	**10**	**0**	**82**
	Individuals	**9567**	**314**	**0**	**9881**
Dik dik (*Madoqua kirki)*	Sightings	1	0	0	1
	Individuals	2	0	0	2
Duiker (*Cephalophus natalensis)*	Sightings	1	0	0	1
	Individuals	1	0	0	1

		Loliondo	Ngorongoro	Serengeti	Total
Eland (*Taurotragus oryx*)	**Sightings**	**19**	**27**	**13**	**59**
	Individuals	**220**	**969**	**279**	**1468**
Elephant (*Loxodonta africana*)	Sightings	0	0	9	9
	Individuals	0	0	140	140
Giraffe (*Giraffa cameoleoparis*)	**Sightings**	**22**	**10**	**8**	**40**
	Individuals	**205**	**33**	**24**	**262**
Grant's gazelle (*Gazella granti*)	**Sightings**	**320**	**333**	**404**	**1057**
	Individuals	**4590**	**9905**	**7725**	**22220**
Hare (*Lepus sp.*)	Sightings	1	3	3	7
	Individuals	1	3	3	7
Impala (*Aepyceros melampus*)	Sightings	7	0	0	7
	Individuals	141	0	0	141
Kongoni (*Alcelaphus buselaphus*)	**Sightings**	**41**	**4**	**255**	**300**
	Individuals	**245**	**14**	**1297**	**1556**
Ostrich (	**Sightings**	**59**	**52**	**81**	**192**
	Individuals	**232**	**508**	**194**	**934**
Reedbuck (*Redunca redunca*)	Sightings	0	0	22	22
	Individuals	0	0	106	106
Shoats (Sheep / goats)	**Sightings**	**9**	**17**	**0**	**26**
	Individuals	**483**	**939**	**0**	**1422**
Steinbuck (*Raphicerus melanotis*)	Sightings	1	1	0	2
	Individuals	1	1	0	2
Thomson's gazelle (*Gazella thomsoni*)	**Sightings**	**747**	**1030**	**882**	**2659**
	Individuals	**17111**	**19493**	**29519**	**66123**
Topi (*Damaliscus lunatus*)	**Sightings**	**15**	**2**	**145**	**162**
	Individuals	**63**	**29**	**644**	**736**
Warthog (*Phacochoerus aethiopicus*)	**Sightings**	**6**	**1**	**72**	**79**
	Individuals	**15**	**2**	**135**	**152**
Waterbuck (*Kobus ellipsiprymnus*)	Sightings	0	0	1	1
	Individuals	0	0	14	14
Wildebeest (*Connochaetes taurinus*)	**Sightings**	**182**	**399**	**57**	**638**
	Individuals	**2530**	**32551**	**6323**	**41404**
Zebra (*Equus burchelli*)	**Sightings**	**214**	**270**	**324**	**808**
	Individuals	**8154**	**5448**	**13917**	**27519**

Density estimation

Table 10 shows the best-fit models describing detection functions for each species. Expected group sizes were calculated for each transect individually therefore the results are not presented here.

Table 10 – Model definition, fit, estimated strip width and coefficient of variance for each species. Strip transect data were all fitted with a uniform function and had a strip width of 200m

		Model definition		Model fit			Strip width	
Species	Region	Key term[1]	Expansions[1]	χ^2	df	P	ESW[2]	CV[3]
Cattle	LGCA	Neg.exp.	None	2.19	4	0.702	443.83	0.146
	NCA	Neg.exp.	None	1.686	5	0.891	481.76	0.354
Eland	LGCA	Half norm.	None	1.383	5	0.926	503.32	0.177
	NCA	Half norm.	None	2.13	3	0.547	945.72	0.205
	SNP	Neg.exp.	None	2.26	5	0.813	799.87	0.373
Giraffe	LGCA	Hazard rate	None	3.732	4	0.444	261.35	1.52
	NCA	Neg.exp.	None	0.829	4	0.934	899.87	0.445
	SNP	Neg.exp.	None	0.657	3	0.883	727.03	0.423
Grant’s gazelle	LGCA	Hazard rate	None	2.63	4	0.622	288.1	0.083
	NCA	Hazard rate	None	2.8	4	0.589	315.63	0.075
	SNP	Hazard rate	None	5.08	4	0.279	286.41	0.087
Human	LGCA	Hazard rate	Herm. Poly. (4)	3.87	3	0.275	78.66	2.631
	NCA	Neg.exp.	None	2.88	5	0.718	268.2	0.227
Hyaena	LGCA	Hazard rate	None	0	0	0	900	0
	NCA	Neg.exp.	None	3.1	4	0.542	76.55	0.341
	SNP	Hazard rate	None	2.41	2	0.299	25.68	4.74
Kongoni	LGCA	Half norm.	None	4.65	5	0.46	417.28	0.115
	NCA	Half norm.	None	0.497	5	0.992	270.39	0.536
	SNP	Hazard rate	None	4.34	4	0.362	357.96	0.1
Ostrich	LGCA	Neg.exp.	None	3.11	3	0.375	238.76	0.153
	NCA	Neg.exp.	None	0.304	5	0.998	434.02	0.176
	SNP	Hazard rate	None	2.89	4	0.576	288.16	0.526
Shoats	LGCA	Neg.exp.	None	3.54	4	0.472	269.45	0.371
	NCA	Neg.exp.	None	3.45	5	0.631	244.84	0.268
T. gazelles	LGCA	Hazard rate	Herm. Poly. (4)	1.06	3	0.786	174.16	0.192
	NCA	Neg.exp.	None	1.362	5	0.928	139.23	0.052
	SNP	Hazard rate	None	0.744	2	0.689	164.28	0.13
Topi	LGCA	Neg.exp.	None	5.14	5	0.3995	184.34	0.282
	SNP	Hazard rate	None	1.44	4	0.837	432.88	0.143
Warthog	LGCA	Neg.exp.	None	3.11	5	0.683	144.24	0.443
	SNP	Hazard rate	None	1.591	4	0.81	161.92	0.396

		Model definition		Model fit			Strip width	
Wildebeest	LGCA	Hazard rate	None	1.928	4	0.749	248.04	0.504
	NCA	Neg.exp.	None	6.48	5	0.262	519.4	0.243
	SNP	Neg.exp.	None	3.34	4	0.503	597.58	0.168
Zebra	LGCA	Neg.exp.	None	1.66	5	0.894	281.68	0.104
	NCA	Neg.exp.	None	2.57	4	0.765	421.19	0.168
	SNP	Hazard rate	None	4.85	4	0.303	554.27	0.141

[1] Models fitted to distance data comprised of a key term with expansion functions added if necessary to get a better fit. Choices of key terms and expansions were restricted to those available in Distance. All combinations of key terms and expansions were tried for each species and model with the best fit was chosen to estimate density.
[2] Effective strip width
[3] Coefficient of variance

Determinants of density variation

Results for determinants of density variation for individual species from GLMs are presented in Table 11. To standardise across species, species densities were then transformed into biomass (kg/km^2) according to published unit values (Coe *et al.* 1976) and GLMs fitted again[1]. Since ages were not recorded during the study biomass was calculated using adult mass only. Biomass was investigated at three levels. Firstly, total biomass was used, representing all species listed in Table 9 except humans. Secondly, biomass was re-calculated excluding zebra and wildebeest since their migratory behaviour caused great variation in the estimates. Although Thomson’s gazelle are also migratory they were not excluded since, unlike wildebeest and zebra, they maintained a presence at some level all year round in all three areas therefore were considered to be important “resident” prey species for carnivores. (Although the full extent of Thomson’s gazelle migratory patterns is not completely understood it is known that in the Serengeti the highest densities are on the eastern plains in the wet season and most move westward during the dry (Maddock 1979) and some remain on the Serengeti plains throughout the year (Durant *et al.* 1988)). Thirdly, biomass was calculated again excluding all livestock. The results for each are presented in Table 12.

Spatial and temporal effects were then investigated further by using the minimal models for each species and biomass estimate to predict the effect of individual terms. Firstly, this was carried out for spatial variation alone, predicting the overall effect of region on densities across the two years of surveying, controlling for all other significant factors. The results for each species were logged to allow simultaneous presentation and plotted in Figure 9. The results for the separate biomass estimates were treated in the same way, except in order to assess the individual species contributions to overall biomass, contributions to raw biomass levels were also calculated and the proportions were then applied to the GLM predictions of biomass. Since this assumes species contribution proportions will be unaffected by factors controlled for in the GLM, the contributions must be seen as approximate. A summary of the results is presented in Figure 10. Finally, predictions were repeated for temporal variation, predicting the effects of year and season within each region on each species and also on the biomass estimates, controlling for any other significant effects. The results for temporal fluctuation are plotted in Figure 11.

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[1] The only species not listed by Coe *et al* was ostrich which was assumed to represent 110 kg.

Table 11 – Summary of GLM results for the effects of potential explanatory terms and their interactions on estimates of density. All terms were fitted to the response variate and removed sequentially until they did not contribute a significant effect to the variance explained by the model. For significant terms ($P<0.05$) χ^2 and P values are derived from having all other significant terms in the model. These terms comprised the minimal model and are highlighted in the table. For non-significant terms, the χ^2 and P values are calculated by adding the term to the minimal model.

Term		Eland		Giraffe		G. gazelle		Kongoni		Ostrich		T. gazelle		Topi		Warthog		Wildebeest		Zebra		Cattle		Human		Shoats	
	Df	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P
Region	2	**50.0**	**0.000**	**149.1**	**0.000**	**28.8**	**0.000**	**61.7**	**0.000**	**45.0**	**0.000**	**16.0**	**0.000**	**25.7**	**0.000**	**56.2**	**0.000**	**196.5**	**0.000**	**19.2**	**0.000**	**217.4**	**0.000**	**37.0**	**0.000**	**83.2**	**0.000**
Road	1	**19.9**	**0.000**	2.1	0.152	**19.7**	**0.000**	0.4	0.530	1.1	0.286	0.5	0.491	3.4	1.680	0.7	0.387	**52.9**	**0.000**	1.5	0.214	**33.0**	**0.000**	2.1	0.145	3.7	0.054
Season	3	**102.4**	**0.000**	**90.2**	**0.000**	**13.7**	**0.003**	**16.3**	**0.001**	3.3	0.069	**23.3**	**0.000**	**10.2**	**0.017**	**12.0**	**0.007**	**228.4**	**0.000**	**72.3**	**0.000**	**12.5**	**0.006**	**69.3**	**0.000**	**55.9**	**0.000**
Time	2	**13.1**	**0.001**	**10.9**	**0.004**	4.8	0.089	1.6	0.455	7.9	0.048	1.0	0.600	5.4	0.069	**10.0**	**0.007**	**54.9**	**0.000**	**8.6**	**0.013**	**13.4**	**0.001**	**9.2**	**0.010**	**54.0**	**0.000**
Year	1	**13.7**	**0.000**	**7.2**	**0.007**	0.1	0.722	**5.4**	**0.020**	1.2	0.555	6.1	0.014	0.8	0.361	**4.9**	**0.027**	0.4	0.537	**34.3**	**0.000**	**72.0**	**0.000**	**6.3**	**0.012**	**8.2**	**0.004**
Region* Road	2	**14.8**	**0.001**	3.8	0.150	3.6	0.166	**6.3**	**0.042**	6.0	0.051	**7.1**	**0.029**	**11.7**	**0.003**	**11.6**	**0.003**	5.4	0.066	**7.0**	**0.030**	1.5	0.477	1.9	0.396	0.0	1.000
Region* Season	6	10.6	0.100	0.0	1.000	**52.0**	**0.000**	10.4	0.107	**42.8**	**0.000**	**47.7**	**0.000**	**31.6**	**0.000**	**17.2**	**0.009**	**39.7**	**0.000**	**68.2**	**0.000**	**15.8**	**0.015**	**19.5**	**0.003**	**19.6**	**0.003**
Region* Year	1	1.7	0.197	12.0	0.062	0.7	0.417	**5.2**	**0.023**	1.7	0.198	**19.3**	**0.000**	1.4	0.241	0.1	0.703	**11.1**	**0.001**	**35.4**	**0.000**	0.0	1.000	0.0	1.000	0.0	1.000
Season* Year	3	2.6	0.449	**22.9**	**0.000**	2.2	0.526	0.8	0.841	4.7	0.197	**11.2**	**0.011**	4.4	0.223	**11.4**	**0.010**	**10.5**	**0.015**	**17.2**	**0.001**	**20.6**	**0.000**	**11.2**	**0.011**	0.0	1.000

Table 12 – Summary of GLM results for the effects of potential explanatory terms and their interactions on estimates of biomass. Biomass was calculated by applying biomass estimates from Coe *et al* (1976) to estimates of individual species density. Significant values are in bold.

Model term	df	Total biomass		Biomass excluding migrants		Biomass excluding migrants and livestock	
		χ^2	P	χ^2	P	χ^2	P
Region	2	**49.0**	**0.000**	**61.4**	**0.000**	**26.9**	**0.000**
Road	1	**14.7**	**0.000**	2.7	0.098	0.0	0.897
Season	3	**102.5**	**0.000**	5.6	0.130	**18.9**	**0.000**
Time	2	**12.0**	**0.002**	3.1	0.216	4.4	0.113
Year	1	**15.7**	**0.000**	**4.4**	**0.035**	1.4	0.240
Region.Road	2	**6.3**	**0.042**	**10.8**	**0.005**	3.6	0.168
Region.Season	6	**68.8**	**0.000**	**20.7**	**0.002**	**27.1**	**0.000**
Region.Year	1	**22.7**	**0.000**	**19.4**	**0.000**	**4.3**	**0.038**
Season.Year	3	**9.3**	**0.025**	6.8	0.080	3.1	0.384

Figure 9 – Summary of GLM-predicted effect of region on species densities estimated by DISTANCE, controlling for any other significant factors (see Table 11). Region explained significant variation in densities for every species. Bars denote standard errors.

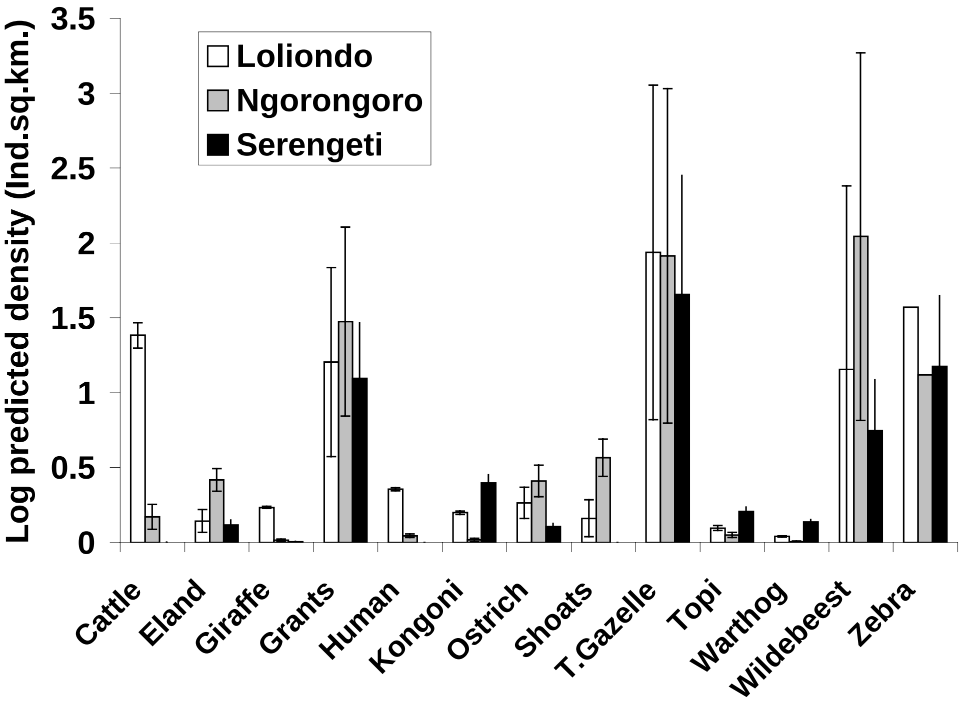
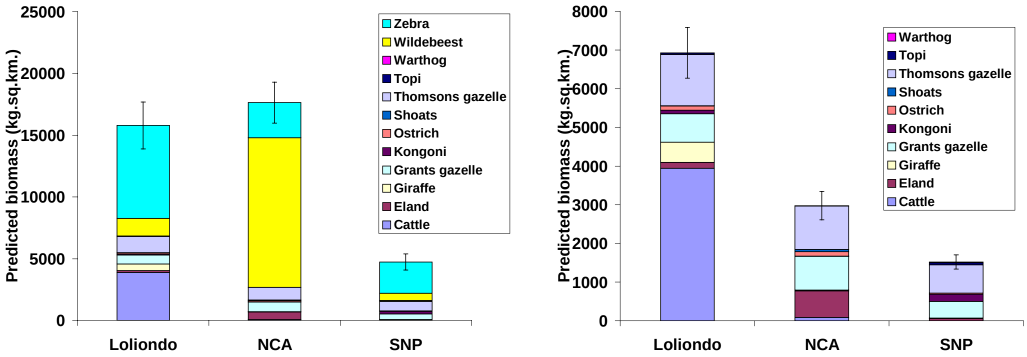


Figure 10 – GLM predictions for total biomass (kg/km^2) of all species with sufficient sightings for density estimation ± standard errors. All predictions control for other factors with a significant influence on density. Predictions have also been subdivided by species contribution, based upon contributions to actual biomass in each region.



All biomass

Biomass excluding primary migrants

Biomass excluding primary migrants and livestock

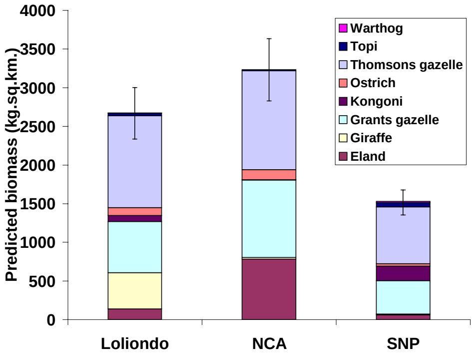
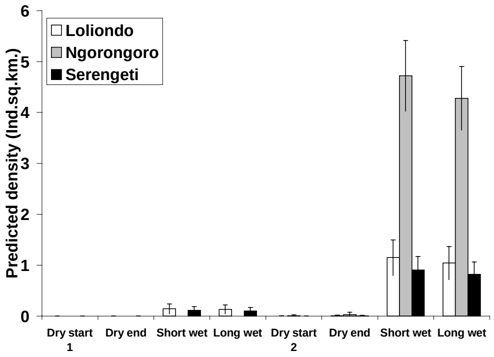
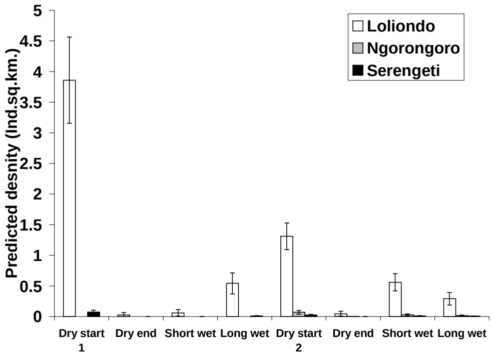


Figure 11 – Temporal variation across seasons and years (1 and 2) in primary herbivore species, livestock and biomass as predicted from Generalised Linear Models, controlling for all other significant factors. Bars denote standard errors.

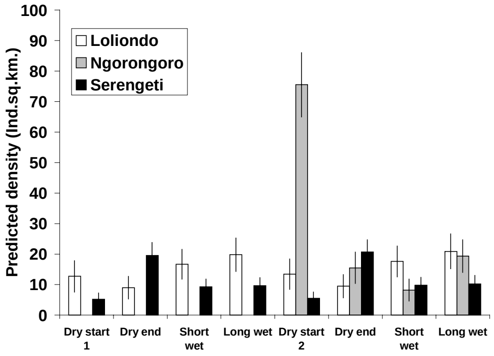
Eland



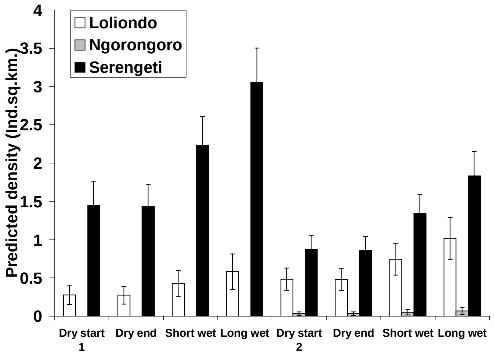
Giraffe



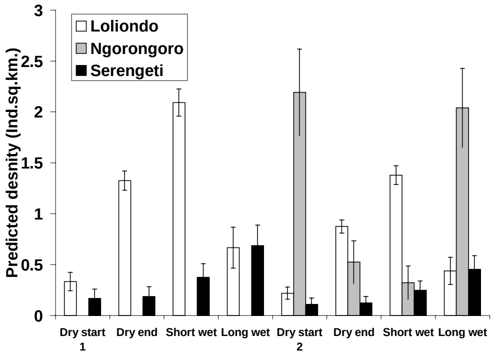
Grant's gazelle



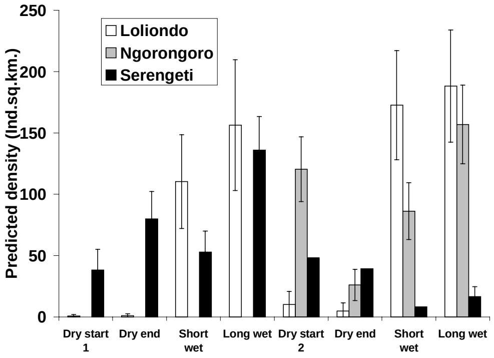
Kongoni



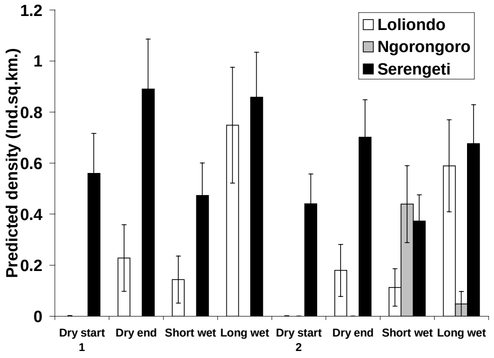
Ostrich



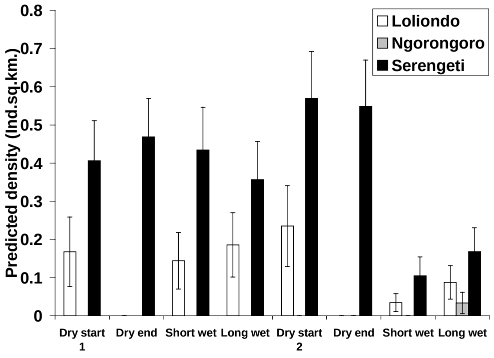
Thomson's gazelle



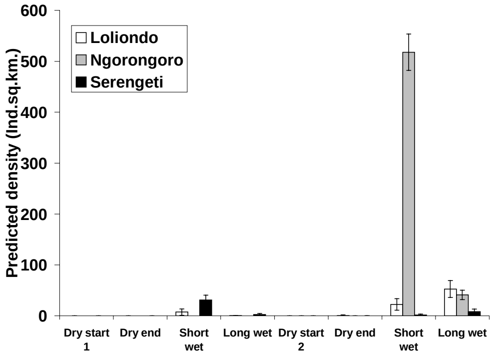
Topi



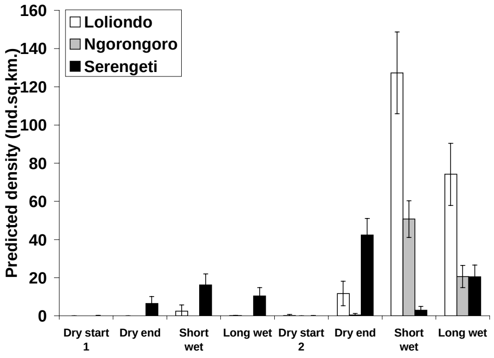
Warthog



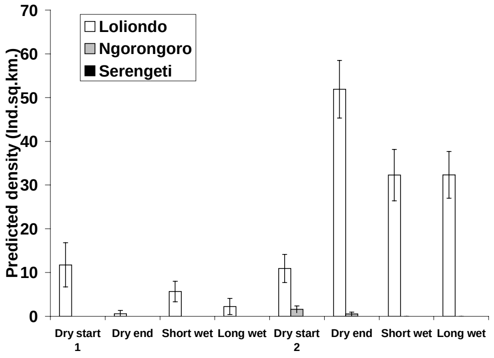
Wildebeest



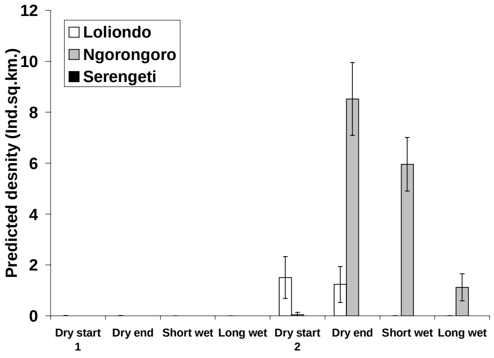
Zebra



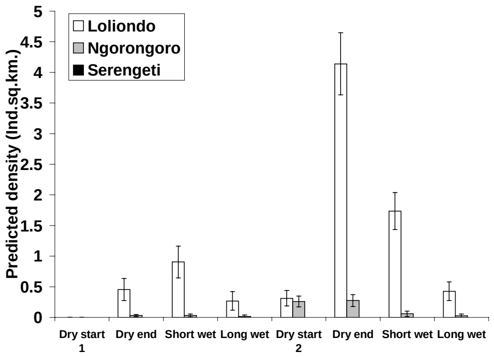
Cattle



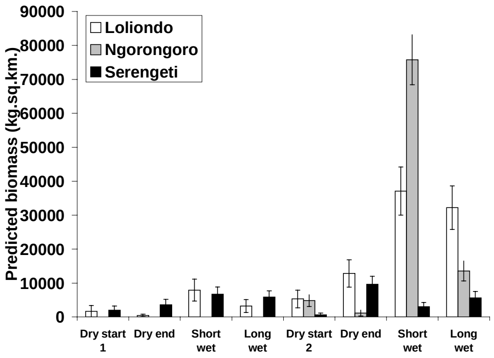
Sheep / goats

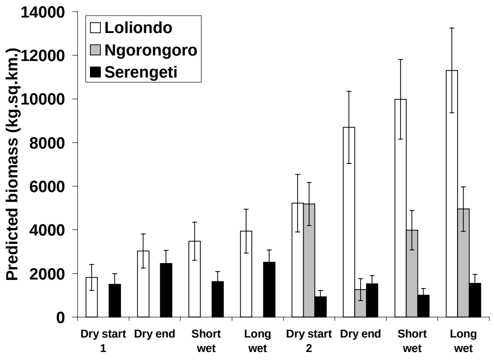


Humans

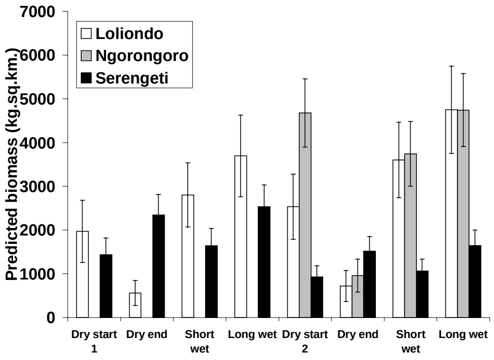


Biomass (total)





Biomass excluding migrants



Biomass excluding migrants and livestock

Results summary by species

Eland

In general, eland were a rare sighting, ranging between 0-5/km^2. Across the survey, there were significant differences in eland distribution (χ^2_2=50, p<0.001) with densities highest in Ngorongoro but not significantly different between Loliondo and the Serengeti. Differences between Loliondo and the Serengeti were also insignificantly different between the two years. Seasonal and annual variation was highly significant with almost no sightings in the dry season in any region (χ^2_3=102.4, p<0.001) and significantly higher sightings in the second year (χ^2_1=13.7, p<0.001). However, temporal patterns did not differ significantly between regions with fluctuations roughly synchronous.

Giraffe

Giraffe were also a rare sighting on the plains, never above 0.1 / km^2 in the Serengeti or Ngorongoro but occasionally approaching 4 / km^2 in Loliondo, aggregating in herds of over fifty animals (*pers. obs.*). Averaging across the survey, there were significant differences in distribution (χ^2_2=149.1, p<0.001) with the highest densities in Loliondo. Seasonal differences were significant (χ^2_3=90.2, p<0.001) with the highest densities at start of the dry season and lowest at the end of the dry season. Seasonal variation was not significantly different between regions. However, seasonal variation was significantly different between years, with lower densities more evenly spread in the second year χ^2_3=22.9, p<0.001).

Grant's gazelles

Of the non-migratory wild species, Grant's gazelles were the most common with survey densities fluctuating around 20 / km^2 and once exceeding 70 / km^2. Differences between region were significant (χ^2_2=28.8, p<0.001) with Ngorongoro having the highest overall densities, but densities were high in all regions and variation between regions was significantly different in each year (χ^2_1=52, p<0.001). Seasonal variation was significant but not as marked as some species (χ^2_3=13.7, p=0.003) and constant between years. However, seasonality varied significantly between regions (χ^2_6=52, p<0.001), with densities highest in Loliondo in the wet, Ngorongoro at the start of the dry and Serengeti at the end of the dry seasons.

Kongoni

Although kongoni occurred in all three regions, there were significant differences between them (χ^2_2 =61.7, p<0.001) with sightings ranging between 0.5 and 3.5 / km^2 in the Serengeti, rarely above 1/km^2 in Loliondo and never above 0.05 / km^2 per survey in Ngorongoro. However, the differences varied significantly with year (χ^2_1=5.2, p=0.023) being more marked during the first year. Seasonal variation was significant (χ^2_3=16.3, p=0.001) with densities increasing from the dry to the wet seasons. There were no differences in seasonality between the regions or years.

Ostrich

Ostrich densities were low relative to gazelle densities, generally fluctuating around 0.5 / km^2 but rising to over 2/km^2 on some surveys. Densities were significantly different between the three regions (χ^2_2=45, p<0.001), with the highest densities in Ngorongoro and Loliondo. Densities varied significantly with season (χ^2_3=7.9, p=0.048) and patterns of seasonality were significantly different in each region (χ^2_6=42.8, p<0.001) with Loliondo densities highest at the end of the dry and beginning of the wet season, Serengeti densities lowest in the dry and highest at the end of the wet season and Ngorongoro densities highest at the end of the wet and beginning of the dry seasons.

Thomson's gazelles

Thomson's gazelles were the most numerous species recorded regularly with survey densities reaching nearly 180 individuals / km^2, a figure only matched by wildebeest densities. Across the whole survey, Thomson's gazelle densities were significantly different across the regions (χ^2_2=16, p<0.001) with overall higher densities outside the park. Temporal fluctuation was the highest of the species that were present year-round with survey densities ranging from 0.8 / km^2 to 188 / km^2 in Loliondo. In the Serengeti, fluctuation was slightly less extreme with survey estimates ranging from 8 to 135 individuals / km^2. Seasonal variation differed significantly between the regions (χ^2_6=47.7, p<0.001) and years (χ^2_3=11.2, p=0.011) with Loliondo having very high densities in the wet season and very low in the dry and Ngorongoro and the Serengeti in particular also peaking in the wet but retaining higher densities in the dry. Densities were higher outside the park in the second year and in the Serengeti in the first year. Thomson's gazelles may be less affected by livestock since they prefer shorter grazing, following in the wake of the wildebeest (Maddock 1979). Springboks, which fill an ecologically similar niche, were also shown to be one of the species more tolerant to human presence due to their ability to graze after cattle (Verlinden *et al.* 1998), (Bergstrom & Skarpe 1999).

Topi

Topi were less common than kongoni or ostrich with survey densities fluctuating below 1 individual per km^2. There were significant differences between the regions (χ^2_2=25.7, p<0.001) with the Serengeti holding the highest densities whilst almost no sightings were made in Ngorongoro. Seasonal differences were significant (χ^2_3=10.2, p=0.017) and significantly different between the regions (χ^2_6=31.6, p<0.001), with sightings in Loliondo and Ngorongoro highest in the wet whilst densities in the Serengeti were highest at the end of the dry and long wet seasons. Seasonal variation did not differ across years.

Warthog

Warthog were one of the least frequent sightings with sufficient data for analysis with densities rarely exceeding 0.5 individuals per km^2 in the Serengeti or 0.2 / km^2 in Loliondo. Differences between regions were significant (χ^2_2=56.2, p<0.001) with the Serengeti having the highest densities and Ngorongoro almost none. Seasonal variation was significant (χ^2_3=12, p=0.007) as was yearly variation (χ^2_1=4.9, p=0.027) and also significantly different between regions (χ^2_6=17.2, p=0.009) and years (χ^2_1=11.4, p=0.01), with densities in the Serengeti almost constant until a fall in the second wet season, densities in Loliondo relatively constant in wet seasons but absent at the end of the dry season and the only sightings in Loliondo in the long wet season.

Wildebeest

Wildebeest reached the highest densities in the survey and the largest range, reaching 518 individuals per km^2 on one survey and zero in others. Differences in region were significant (χ^2_2=196.5, p<0.001) with the highest overall densities recorded outside the park. Temporal variation was extreme within and between all areas and across years but wildebeest were completely absent from all surveys in the dry season in all areas.

Zebra

Zebras followed similar patterns to the wildebeest with extremely high (127 individuals per km^2) densities on some surveys and absent from others. Regional differences were significant (χ^2_2=19.2, p<0.001) with Loliondo showing the highest densities. Seasonal and annual variation were significant within and between regions and followed similar patterns to the wildebeest except for an earlier arrival on the plains at the end of the dry season to different extents in all three regions and very occasional sightings at the end of the dry season.

Cattle

Cattle only occurred in significant numbers in Loliondo where they reached average densities roughly equivalent to Grant's gazelles (around 20 individuals per km^2). Differences in region were highly significant (χ^2_2=217.4, p<0.001) because cattle were banned from the Serengeti and only used on the Ngorongoro grasslands at low levels. Temporal variation occurred both seasonally (χ^2_3=12.5, p=0.006) and annually (χ^2_1=72, p<0.001) with Loliondo grazing occurring at the start of the dry and during the wet season in the first year and the end of the dry and through the wet season in the second year. Grazing was limited to the dry season in Ngorongoro. Cattle densities were much higher in the second year of the survey in Loliondo (data are not available for Ngorongoro).

Sheep / goats

At their maximum in Ngorongoro, sheep and goat densities exceeded most other species excepting migrants and Grant’s gazelles. However, they were generally absent from Loliondo and completely absent from the Serengeti. Differences in region were therefore significant (χ^2_2=83.2, $p<0.001$). Seasonal and annual variation was significant (χ^2_3=55.9, χ^2_1=54, $p<0.001$) and seasonal variation was different between Ngorongoro and Loliondo with grazing occurring in Loliondo during the dry seasons and in Ngorongoro from the end of the dry to the end of the wet seasons.

Biomass

Estimates of total biomass showed significant differences between regions (χ^2_2=49, $p<0.001$) with areas outside the park containing a significantly higher census average. Much of the difference in total biomass was explained by the large numbers of migratory species. Since the value and accuracy of the migrant biomass is questionable (see discussion) they were removed from the analysis. However, after removal the difference was still significant (χ^2_2=61.4, $p<0.001$) with Loliondo having the highest biomass exclusive of migrants. The species composition bars showed cattle contributed a large proportion of the difference but even when livestock were removed there were still significant differences in biomass (χ^2_2=26.9, $p<0.001$) with the National Park containing the lowest. Seasonal variation within and between regions was significant for biomass estimates excluding livestock and migrants, with the Serengeti peaking at the end of the dry and wet seasons, Loliondo peaking during the dry season and Ngorongoro was high at all times except the end of the dry season. However, seasonal variation was not significant when including livestock in the analysis since they appeared to buffer changes, with higher densities when other species were at low density. Finally, whilst seasonal variation was relatively constant across years, regional differences between years were significant, primarily due to the steady increase in cattle presence in Loliondo during the census.

3.5 *Discussion*

Differences in species richness between the national park and its buffer zones

Over two years, the line transect surveys showed no major differences in the species present inside and outside the park, with most differences recorded attributable to local habitat differences (*e.g.* reedbuck, waterbuck and the Neotragini and Cephalophini antelopes). All species commonly seen in the ecosystem were present in all three sites and there was therefore no evidence that the presence of the Maasai and their livestock was particularly detrimental to any single species included in this survey. Elephants (Douglas-Hamilton 1987), (Western 1989) and buffalo (Hofer *et al*. 1996) were the species most likely to be absent outside the park based on previous literature but neither are typically open grassland species and were not covered in any detail by the transects. Nevertheless, both species were sighted outside the park on several occasions during the study.

Differences in species abundance and biomass between the national park and its buffer zones

The survey showed that although density varied significantly between regions, no single region contained higher densities of all species. Comparing overall density between the three sites across the two years of study showed the Serengeti National Park to have consistently higher densities of kongoni, topi and warthog only. In Loliondo there were significantly higher densities of giraffe and Thomson’s gazelles and Ngorongoro showed higher densities of eland, Grant’s gazelles and ostrich. Of the migrants, wildebeest were overall at highest density in Ngorongoro and zebra in Loliondo whilst cattle and people on foot were at highest densities in Loliondo and sheep and goats were most common in Ngorongoro. The density of most species fluctuated widely throughout the study. The only species that remained consistently different were kongoni, topi and warthog which were only ever present in very low densities in Ngorongoro and relatively low densities in Loliondo, compared to the park, and giraffe which were most common in Loliondo. The absence of kongoni, topi and warthog from Ngorongoro is likely to be at least partially explained by the difference in rainfall. In comparison to the gazelles and eland, the Alcelaphini tribe and warthogs are more dependent on water (Estes 1991), a fact supported by the increase of topi in Ngorongoro in the short wet season. However, other reasons are also likely to be important, since of the two species, it is the kongoni that is least water-dependent (Estes 1991) yet kongoni were only ever sighted rarely in Ngorongoro. It might also be significant here to note the findings of Caro (1998) who showed the species most affected by tourist hunters in Tanzania to include kongoni and warthog (Caro *et al*. 1998b). The LGCA was one of the most intensively hunted areas in the early 1990s (Caro *et al*. 1998b) and hunting concessions are still in use today, however, commercial hunting is not allowed in Ngorongoro therefore hunting cannot explain all of the variation. The difference in giraffe density is even harder to explain. As browsers, giraffes were not expected to be regularly sighted in the open areas included in the survey and therefore the low densities in the Serengeti and Ngorongoro were expected. It might be suggested that giraffe differences were due to the differences in habitat around the study areas, with the Loliondo site closer to wooded habitat and interspersed with trees and shrubs, yet fairly frequently aggregations of up to sixty were seen in the middle of treeless short grass plains.

Furthermore, the National Park did not have the highest overall biomass estimates for the period studied. For total biomass, areas outside the park had significantly higher estimates. However, a large proportion of the difference was contributed by wildebeest and zebra which were not represented at particularly high levels inside the park by this survey (see “Limitations of the study”, p.98). Nevertheless, biomass estimates were still significantly higher outside the park when wildebeest and zebra were excluded from the analysis, possibly lending some support to tentative ideas that pastoralism can allows more efficient use of land than wild species alone (Osterheld *et al*. 1992). In addition, there was no evidence that livestock biomass replaced wild species biomass outside the park. By removing wildebeest, zebras and all livestock from the analysis and comparing only wild species with a year-round presence it was shown that there was still a higher biomass outside the National Park than inside, represented predominantly by Grant’s and Thomson’s gazelles, although results were also strongly influenced by high densities of large-bodied eland in Ngorongoro and giraffe in Loliondo.

Temporal variation in species abundance

Temporal variation was important for almost all species. Overall, all species densities varied significantly with season or year, with variation most marked in species expected to migrate, although variation also occurred in resident species showing that local movements were significant at the scale of this study (for example, many species in Loliondo move into the woodland areas during the dry season and return to the plains from November onwards (Watson 1969)). Seasonal variation also occurred for total biomass (as the wildebeest and zebras came and went) and also for biomass excluding migrants and livestock, but biomass estimates *including* livestock did not vary significantly with season since livestock numbers tended to rise when wildlife densities fell. In general, abundance was higher during the wet seasons. However, a simple summary of the timing of seasonal variation is not possible since seasonal variation was different in each region for all species except eland, giraffe and kongoni and also varied by year for giraffe, Thomson’s gazelle, warthog, wildebeest, zebra, cattle, humans and total biomass. The differences in seasonal variation between regions meant that fluctuations in density were not synchronised in all areas. For example, kongoni showed a marked increase in the Serengeti during the wet season but numbers in Loliondo varied little between the seasons. In contrast, topi showed a marked increase in Loliondo in the long wet season but were relatively constant inside the park. Ostrich also differed, peaking in the Serengeti in the long wet season, in Loliondo in the short wet and in Ngorongoro in the long wet and dry start whilst Thomson’s gazelle were highest in the dry start in Ngorongoro when they were scarce elsewhere but peaked in the second long wet season in the Serengeti. Annual differences were more constant with all but Grant’s gazelle, topi, ostrich and wildebeest showing significantly higher numbers in the second year. However, seasonal differences also varied by year, for example giraffe densities were highest in Loliondo in the long wet and dry start periods, but highest in the short and long wet in the second year. Yearly differences were particularly evident in livestock with cattle presence high at the end of the dry season in year 2 but not year 1 whilst sheep and goat densities increased in Loliondo in the dry season of year 2 but were almost entirely absent from Loliondo grasslands in year 1.

The implications for carnivore prey base outside the National Park

The results of this survey show that, in the areas studied, the simple presence of the Maasai and their livestock does not necessarily lead to any major change in prey availability for large carnivores. Species richness was equivalent outside the park and densities of the preferred prey of the primary large carnivore species (cheetah: Thomson's gazelle (Caro 1994), hyaena and lion: wildebeest (Kruuk 1972), (Schaller 1972b)) were all higher on average outside the park over the two year period. Biomass of prey availability was also higher on average outside the park, with biomass of wild, resident prey at over 2000kg/km^2 for most of the year. However, the key period for carnivore ecology is the time of minimum prey availability *e.g.* (Scheel & Packer 1995). This occurred in all areas at the end of the dry season and availability of wild herbivores was highest inside the National Park at this point, which could have important implications for the maximum carnivore population capacity or movement patterns. However, if livestock are included in the analysis of biomass, it can be seen that biomass during this crucial period is in fact higher outside the park. If carnivore populations were equivalent outside the park, and limited by resident prey, this might hold important implications for livestock predation.

Comparisons with previous data

Variation in methodologies, coverage and timing and large confidence limits mean that accurate comparisons between many of the Serengeti surveys is problematic (Campbell & Borner 1995), (Perkin 1995). Furthermore, comparisons of ground-based surveys and aerial surveys are thought to be of limited value, with aerial surveys tending to under-estimate higher densities (Caro 1999b). Nevertheless, in the only comparable study of herbivores in Loliondo compared to the Serengeti, Watson (1969) used an aerial census to calculate almost identical biomass estimates of 3907 kg/km^2 in Loliondo and 4027 kg/km^2 in the Serengeti, although the bulk of the migratory wildebeest and zebra were not included in the survey. These figures are comparable to the results of this study for Loliondo in the first year of this survey with estimates of just under 4000kg/km^2 but are higher than either year of Serengeti estimates which fluctuated around 2000kg/km^2. However, they were dwarfed by the second year estimates for Loliondo which exceeded 10,000kg/km^2 as cattle numbers rose. Watson suggested that although overall biomass inside and outside the park was similar, cattle (1834 kg/km^2) replaced the short grass feeding wildebeest, zebras and gazelles (Loliondo: 1228 kg/km^2 , Serengeti: 2907 kg/km^2) (Watson 1969). Results from this study do not support this, with higher densities of Thomson's gazelles, wildebeest and zebra in the same year cattle densities rose by a factor of 4-5 and long grass feeders (topi and kongoni) less common outside the park. Comparisons can also be made with data from elsewhere in Tanzania. Species richness in this study was shown to be equivalent inside and outside the park. In previous studies, this has not always been the case. For example, Caro (Caro 1999d) found just 16 of 24 species from the Katavi National Park in the neighbouring Game Controlled Area buffer zone, and 8 of 24 species in a Forest Reserve and complete open access buffer zone, although his study included habitats other than grasslands. Furthermore, this study showed equivalent or higher levels of biomass outside the park compared to inside over the course of the study. Again, this contrasts with Caro's findings who found wild biomass was one third of the National Park (although, it should be noted that the species most affected were the megaherbivores not covered in this study, the hippopotami, elephants). However, there were also some areas of agreement; of the buffer zones Caro studied, the Game Controlled Area was the healthiest with higher overall biomass and densities of giraffe, buffalo, zebra and warthog than a logged Forest Reserve and a completely open access area. This was despite the Forest Reserve having low densities of pastoralists in comparison to the other buffer zones.

Further implications

Two further points arise from these data that are particularly important. Firstly, the aim of this study was to try and determine whether prey availability for carnivores was higher inside the park or outside the park. However, this approach tended to assume some sort of stability to the system; that a summary of two years' data would enable temporal variation to be accounted for and a single density for each region assigned. The reality was that this situation did not exist. The factors driving herbivore movements (primarily rainfall *e.g.* (Maddock 1979), (Durant *et al*. 1988) were not predictable enough to show a single temporal effect constant between regions or years. In other words, it is very hard to summarise any sort of single representation of herbivore density, even for a given season, for comparison inside and outside the park since seasonal variation differed by year, by species and by region. Estimates of average densities across the two years obscure periods of very high or low abundance whilst estimates restricted to a single season could vary wildly depending on whether the start or end of the season was surveyed, the species in question and the year. It would in fact be possible to show almost any species to be more common inside the park or outside the park depending on how the data were selected or when they were surveyed. Rather than representing three distinct regions that can be compared, or even a gradient with decreasing protection, it appears that the three areas selected in this study represent three equally important components of a highly dynamic and unpredictable system, with one area holding higher species densities and biomass during periods when another is low. This system is operating despite the presence of Maasai and their livestock – if they have any effect, it does not seem to be as important as the abiotic effects that are thought to drive herbivore movements.

Secondly, these results could hold important implications for the theory of rangeland dynamics since these data do not support the idea that a single carrying capacity can be determined or measured for any of the areas studied as applied by some authors *e.g.* (Brown 1971), (Coe *et al*. 1976), (Lamprey 1983), (Fritz & Duncan 1994), (Mizutani 1998). Rather they support the ideas that semi-arid rangelands exist at a variety of carrying capacities, fluctuating widely with unpredictable rainfall and weather patterns and never reaching equilibrium (Sandford 1982), (Homewood & Rodgers 1987), (Behnke & Scoones 1993), (Warren 1995).

Limitations of the study

The first limitation of the study was that the study areas were not identical in their habitat composition, as discussed in chapter 2. In an attempt to overcome this, only data from transects carried out in predominantly open areas were used. However, this still leaves the possibility that the open areas surveyed will be affected differently by the availability of nearby habitat. To overcome this, the preferable solution may have been to survey all habitats both inside and outside the park and to then include habitat as a variable in the analysis. A second criticism along similar lines is that rainfall was not taken into account, despite recognition of its strong influence on herbivore distribution *e.g.* (Maddock 1979), (Durant *et al*. 1988). Efforts were made to collect rainfall data throughout the study but were unsuccessful. Although rainfall in Loliondo and Ngorongoro is similar to the Serengeti plains (Watson 1969), (Sinclair

1979) the differences that will have occurred may have explained some of the variation recorded.

A third criticism is that the methods used did not appear to be good for estimating zebra or wildebeest density. Not only did the high densities cause problems with counting and the associated limitations associated with a change to strip transect sampling, but both of these species are migratory, moving onto the plains from the northern and western areas of the ecosystem during the wet season, the exact timing and location being determined by highly variable rainfall patterns (Maddock 1979). Since the survey technique used in this study sampled only a small proportion of the spatial and temporal range of these migrants it was clear that the wildebeest and zebra were not sampled sufficiently. For example, the main bulk of the migrants were present in the Ngorongoro study are during one survey, giving very high estimates, but the surveys in the Serengeti did not happen to coincide with any periods that the highest densities were present in the study area, although on occasions several thousand were present within a few kilometres whilst the study area happened to be almost empty.

Various limitations also exist in the line transect methodology itself, including distribution of sightings in relation to the observer, accurate application of detection probability models, accurate distance measurements, observer bias and problems associated with multi-species surveys (Buckland *et al*. 1993). Firstly, it is assumed that sightings are distributed randomly with respect to the line, allowing densities calculated when detection probability equals 1 to be representative of the area as a whole. This assumption can be violated by animals moving away from (or towards) the survey vehicle, or by the use of roads which rarely cover a representative proportion of the study area and can affect species distribution by their very presence. In this study, movement in relation to the vehicle did occur to some extent but was generally limited to a few metres, even outside the park. This was accounted for by careful study of sightings histograms before use, setting intervals to avoid a peak at any distance away from the line. Roads were controlled for by including a mix of road and non-road transects in the survey and including them as a variable in the analysis models. Although roads did have both significant positive and negative effects on several species (Maddox, in prep.) these could then be controlled for in the analysis.

Further limitations occur due to the trade-off between the requirement for sufficient sightings to enable accurate detection probability modelling (60-80) and the requirement to fit separate detection curves to different conditions. In this study, data were sufficient to fit separate detection curves to each species and to limit analysis to a single habitat. However, data pooling was required across time since few species had sufficient sightings within a single survey. This required the assumption that detection probability was unaffected by grass height and vegetation colour or any other variable that may vary over time. Although both variables were recorded during the survey, they could not be added to the analysis due to correlation with season. However, it is unlikely that the sighting probability for most of the large herbivores would be affected by this, with the possible exception of warthog.

Distance measurements are probably the most likely source of bias, although they were supported by use of a range finder at close distances and regular practice for longer distances. Nevertheless, it would have been preferable to use tools that could have accurately measured distance to 1000m+ such as a thermal imager (Gill *et al.* 1997). Observer bias was not present since only one observer was used. Precautions must also be taken with multi-species surveys such as this, with some arguing reduced effectiveness for some species such as eland, zebra and livestock densities (Caro 1999d). A further assumption is that all species are identified correctly in every instance. For most species at most distances confident identification was possible with the use of binoculars. However, there was potential for confusion between gazelle species at long distances. Since all species datasets were truncated before analysis removing at least 5-10% of the outliers (Buckland *et al.* 1993) it is assumed this effect was negligible. Further problems were removed due to the size of the dataset so that no common detection curves were fitted across species and rarer species had sufficient sightings for accurate analysis.

Although the study includes some limitations, estimating densities of large herbivores across such large areas is always going to require some assumptions. This study surveyed herbivores inside and outside the park over two years using the relatively new methods of distance sampling. No surveys of a this scale or using these methods have been used before to compare densities across differing protection regimes and the data presented on the differences and fluctuations in density provide important new information on the effect of pastoralists on ungulates and on the potential prey availability for large carnivores outside the Serengeti.

Chapter 4: Variation in large carnivore abundance inside and outside the Serengeti National Park

4.1 Summary

In previous studies, large carnivores have been shown to be far more successful in core-protected areas. In this chapter, the numbers of medium and large carnivores inside the national park study site are compared with the Loliondo and Ngorongoro sites outside the park to test whether numbers are significantly lower in the pastoralist buffer zones. Two methods are employed; call-ins are used to attract scavenging carnivores whilst individual recognition is used to estimate the abundance of cheetahs, which do not respond to call-ins. 221 call-ins were conducted over two years. Calibrations were carried out on 22 lion groups and 11 hyaena groups to determine chance of response and effects of wind, thus enabling estimates of density. Twenty-one different species responded, six of which were mammalian carnivores. The only differences in species diversity were responses of side-striped jackals inside the park and striped hyaenas outside. All other species were recorded inside and outside the park. Spotted hyaenas were the most likely to respond, occurring at 80% of all call-ins. More black backed jackals responded outside the park in Loliondo than inside (χ^2_1=20.54, p<0.001). More golden jackals also responded outside the park in Ngorongoro than inside (χ^2_1=10.28, p<0.001). Chances of a hyaena response were equivalent in all areas, but more hyaena individuals responded inside the park than in Loliondo (χ^2_1=16.69, p<0.001) with density estimates of 0.74/km^2 compared to 0.34/km^2 but responses were equivalent in Ngorongoro. The number of lion responses was equivalent inside and outside the park (χ^2_2=0.43, *NS*) with density estimates in Loliondo averaging at 0.37/km^2 and 0.21/km^2 inside the park. 88 independent cheetahs were recorded in the park, 24 in Loliondo and 19 in Ngorongoro. However, data were insufficient for CMR analysis and recapture rates suggested that only a small proportion of the population had been sighted. The results therefore show that large and medium carnivores are surviving successfully outside the protection of the National Park. Lion numbers were especially high, comparable to peak estimates from the Serengeti in the 1970s and even to peak densities elsewhere in Africa although estimates were not necessarily representative of the uncensused areas.

4.2 Introduction

Carnivores outside protected areas

Most large carnivores are currently threatened by a range of factors, primarily human-driven since they can directly compete with or threaten humans (Woodroffe 2000) but also because their behavioural ecology dictates that they live at low densities and require large areas to survive (Woodroffe & Ginsberg 2000). Consequently, direct persecution by humans is thought to be the primary threat to many large carnivores (Woodroffe & Ginsberg 1998) and the basis of most carnivore conservation programmes is the provision of core-protected areas that remove the threat from humans. (For a complete review of carnivore conservation and individual species' conflict with humans, see Chapter 1). This negative relationship with human presence is not new. In Europe, the 18th and 19th centuries saw the extinction of brown bears, lynx and wolves from most areas of high human density due to persecution and environmental change (Breitenmoser 1998) and now the same situation is being recorded in Africa. Analysis of human density and carnivore extinction has shown that, in general, carnivore extinctions rise with increasing human populations (Woodroffe 2000). However, the strength of the relationship between human density and extinction has been challenged (Linnell *et al*. 2001) and it is acknowledged that local management, culture, governmental policy and trade can have overriding effects (Linnell *et al*. 2001), (Woodroffe 2000). Thus, in some areas, large carnivores can and do survive in areas inhabited by people, for example in the Swiss Alps brown bears, lynx and wolves are returning naturally or being reintroduced into areas also occupied by farmers (Breitenmoser 1998) or lions in Tanzania (Creel & Creel 1997). In some cases it has even been suggested that certain carnivores may survive more successfully outside National Parks, for example wild dogs (Mills & Gorman 1997) or cheetahs (Laurenson 1995b). Indeed, the majority of cheetahs are thought to live outside protected areas (Marker 1998) due to the conflict with lions and hyaenas inside protected areas (Laurenson 1994). The most extreme example of this can be seen in Namibia where over 90% of the approximately 2500 cheetahs live outside protected areas on commercial farmland where they occasionally take small stock and calves up to six months old (Marker-Kraus 1997)

Carnivore abundance in the Serengeti buffer zones

Perhaps due to the scarcity of carnivore populations in semi- or unprotected areas or the difficulties associated with studying small and shy populations, very little work on carnivores outside National Parks has been conducted, including the Serengeti ecosystem. One exception is a helicopter lion survey that was carried out in the Loliondo Game Controlled Area in the 1990s by Frankfurt Zoological Society. This indicated that lions were present outside the park but were limited to a zone within 8 km of the park boundary and absent from areas around Maasai bomas. Furthermore, sex ratios and age structure were highly skewed with seven females for every male and only one adult male, whilst only 6% of sightings were cubs, compared to a ratio of 2:1 and 27% cubs inside the park (Borner 1992). Most recently, Whitman (*pers. comm.*) conducted a survey of lions in the Maswa Game Reserve to the south of the park showing lions to be present, but intensively hunted. No surveys of hyaenas or cheetahs have been conducted outside the park, although it has been hypothesised that hyaena populations throughout the Serengeti ecosystem suffer from high mortality outside the National Park through snaring (Hofer & East 1995), a factor that is presumably applicable to other large carnivores too, but that the buffer zones may form an important refuge for cheetahs from the high lion and hyaena densities inside the park (Laurenson 1995b).

Censusing carnivores

A wide range of survey techniques exist for censusing carnivore populations (for a review of census techniques in general, see Chapter 3; for a review of techniques used for carnivore surveying see Chapter 5). For this census, two primary methods were employed. Call-ins are a widely used method for surveying carnivores, using taped recordings, such as hyaena calls, to attract animals to the speaker. The technique was originally developed for hyaena censusing and used either in conjunction with individual recognition (Kruuk 1972) or as a direct census tool (Creel 1996), (Creel & Creel 1997), (Mills & Gorman 1997), (Mills 1998), (Mills *et al*. 2001), (Sillero-Zubiri & Gottelli 1992). Call-ins have also been used to attract lions in conjunction with capturing (Smuts 1977), individual recognition (Whitman, *pers. comm.*) and to census lions directly (Creel 1996), (Mills & Gorman 1997), (Ogutu & Dublin 1998). Accuracy of call-ins can be high if calibrated properly. In the Masai Mara National Reserve call-in estimates were shown to be less than 1% different from total counts and precision for hyaenas thought to be at least as high due to their more uniform response (Ogutu & Dublin 1998). However, cheetahs do not respond to the recordings that attract lions and hyaenas since they are the only large predator in the Serengeti not to scavenge (Bertram 1979), (but see (Caro 1982) for an exception) and avoid larger carnivores (Durant 2000b). Therefore, individual recognition techniques were also used. Long-term studies with individual identification of all or most animals present within a given area have been used to census several carnivore species including lions in the Serengeti and Ngorongoro (Hanby *et al.* 1995), (Pennycuick 1970) cheetahs in the Serengeti study (Caro 1994) and wild dogs in South Africa (Maddock & Mills 1994). Cheetahs can be individually recognised from their spot patterns (Caro 1994), (Cooper & Durant, in press). Leopards, wild dogs and the smaller cats were also all present in the study area but not included in the survey since they required completely different census techniques.

Chapter aims

In order to examine the differences between large carnivore abundance inside and outside the park, three primary questions were investigated:

1. Does large carnivore diversity differ outside the park? Are there any species present in the core-protected area that do not survive outside the park?
2. Is abundance of large carnivores different outside the park from inside? Do the buffer zones support lower densities of large carnivores?
3. Are the differences in density equal for all species or do some show greater differences from park populations? Does this support the potential of Maasai buffer zones as refuges for cheetahs?

4.3 Methods

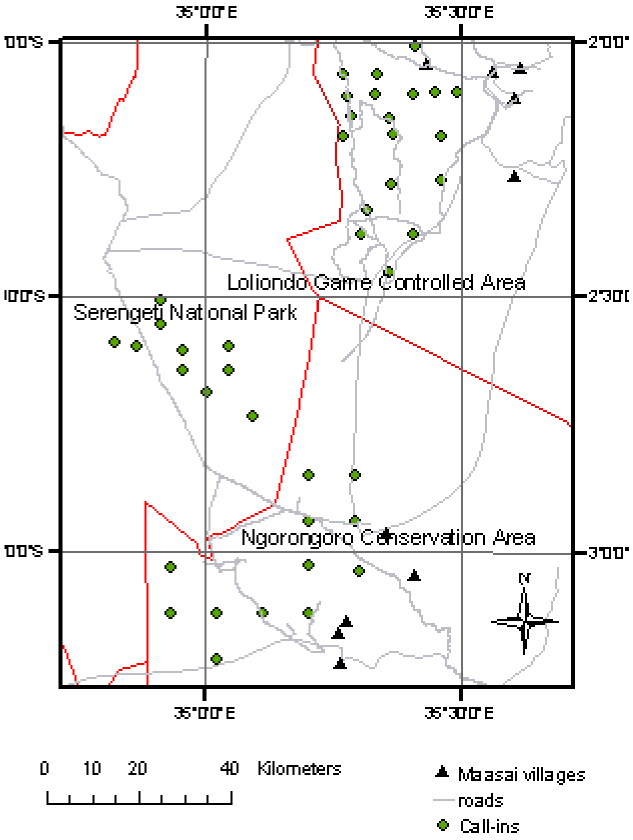
Call-ins

Placement and coverage

Call-ins sites were determined by randomly selecting map grid intersections on 1:50000 maps for each of the study sites. If the random site was inaccessible or had poor visibility it was moved to the closest suitable point, ensuring all call-ins had clear visibility for at least 500 metres in all directions. Minimum distance between sites was determined by the known response distances for each of the target species and a requirement to maximise area coverage. Lion responses have been shown to occur up to 2.5 km (Ogutu & Dublin 1998) and an effective luring range was found up to 4 km in South Africa when a carcass was used as bait (Smuts 1977). However, the audible response zone for hyaenas can extend up to 3.7 km in the right conditions (Creel 1996). Sites were therefore never within 5 km of the next nearest site (following the methods of Ogutu and Dublin (1998) and Whitman (*pers.comm.*)) and most were at least 10 km apart to avoid any chance of interference between call-ins. It has been shown in a previous study that call-ins need only cover 20% of an area to provide accurate estimates of the overall density (Ogutu & Dublin 1998). Sufficient call-ins were therefore carried out in each study area to cover at least 20% of the area.

Surveys took approximately one month to cover the three study areas and were repeated quarterly to enable coverage of the main seasonal variation in the Serengeti using the same call-in sites for each survey round. The time periods covered were; January (mid short rains period), April (mid long rainy season), July (beginning of the dry season) and October (end of the dry season).

Figure 12 – Positions of call-ins in the three study areas. Red lines show the protected area borders.



Protocol

The call-in recording consisted of fifteen minute segments comprising three minutes of a wildebeest in stress (recorded by G. Mills originally on analogue equipment) followed by 12 minutes of approximately 20 hyaenas and one lion squabbling at a kill (recorded by J. Grinnell on analogue equipment). Four of these segments were combined to make a tape exactly one hour long. Recordings were played back at the call-in site at a peak sound pressure of 114 dB at 1m using a Sony TCD8 Digital Audio Tape player with two Martin Audio Studio monitor loudspeakers (one W2, the other CD2 but adjusted to give the same output) mounted facing opposite directions on a Land Rover roof. Each call-in was begun as early in the morning as light restrictions allowed, which generally mean the first began between 06:00 and 06:30, and the second between 7:45 and 8:15. No call-ins were started after 09:00 so that all call-ins were played in a time period where large predators could reasonably be expected to be active. Call-ins were not carried out in the evening since failing light meant responding animals were hard to spot or photograph. Prior to the call-in start the temperature, wind, weather and grass length were recorded. Once the call-in had begun a Psion hand-held computer was used to record animals in real time as they were seen with binoculars from the car, recording the species, number and sex composition of approaching groups, distance first seen and closest distance approached. Two measures of responses were kept. Firstly, a count of all new arrivals was made. Secondly, a running total of animals in sight was kept. In both cases, sightings were limited to a radius of 500m. The first measure took into account animals leaving before new arrivals were spotted, a common occurrence given the length of the call-in. However it included the risk of animals leaving and returning to the speaker and being counted twice. The second measure gave a confident estimate of the minimum responses, but did not include animals not present at the same time and therefore may have underestimated the total. To reduce the error of the first measure, new sightings were classified as "arrivals" - animals that could be confidently classified as new, and "returns" - animals that could not be confidently classified as uncounted. "Returns" therefore contributed to the running totals but not to the count of new arrivals. Distinguishing between arrivals and returns was simple for lions, which were individually recognisable, and classified by behaviour for hyaenas and jackals. Animals that were running towards the speaker, or arrived from a new direction, were classified as "arrivals". Animals that appeared uninterested or arrived from a direction where similar animals had just departed were classified as "returns". Analysis of responses was carried out on the number of individual arrivals rather than the maximum present at any one time since animals frequently arrived at the call-in after others had left whilst the running total of animals present was used to analyse behaviour at the call-in (see Appendix III, p.357). Data logging and scanning for arrivals was carried out continuously. At fifteen minute intervals the car was turned ninety degrees to give an even sound distribution and once the call-in was complete the end temperature and wind speed were recorded.

Calibrations

Call-ins have been found to be effective as estimators of absolute predator numbers if calibrated, assessing factors that influence variability of response and testing the reliability of call-back estimates with independent estimates of known accuracy (Ogutu & Dublin 1998). Although response range has been calculated for both lions and spotted hyaenas (Mills *et al*. 2001), range is likely to vary widely with habitat and therefore it has been recommended to recalculate for each survey (Mills *et al.* 2001). In order to quantify the responses recorded for call-ins, calibrations were carried out on lions and spotted hyaenas to determine the audible range of the experiment, the effect of wind strength and direction and the chance of response for different ages and sexes. Calibrations were carried out using an identical method to call-ins, except that locations were determined by locating a target species before the call-in began, recording the distance and direction between the calibration animal and the speaker and, the subject sex, age, belly size (lion belly sizes were estimated on a scale of 1-5, similar to cheetahs – see Chapter 2 for details), local habitat and the presence of cubs. However, for hyaenas, neither sexing, belly size estimation nor accurate age estimation was possible. In general, as wide a range of directions and distances as possible was tried for both species. Some calibrations were carried out with two observers, one staying with the target species, continuously recording responses to the call-in (looking, moving towards or moving away) and one carrying out the call-in. When calibrations were carried out by one observer, photographs of the target species were taken to ensure correct identification if it arrived at the call-in, but continuous behaviour could not be recorded. In general, calibrations were carried out in the months between the main call-in surveys. However, several were carried out during the surveys by spotting an animal whilst travelling to a call-in station, photographing it and comparing to photographs of animals that arrived. All calibrations were carried out before 9:00 am and for calibrations not carried out in conjunction with a survey the tape was stopped once the target animal arrived (within 500m) at the call-in to minimise habituation which could affect the actual surveys. All calibrations were carried out in the Serengeti where carnivores could be readily found without the use of call-ins. Only the four species that most regularly responded to call-ins were included in the analysis; black backed jackals, golden jackals, spotted hyaenas and lions.

Individual recognition of cheetahs

In general, surveys based upon individual recognition do not search areas randomly and equally, instead they try to maximise the number of sightings made (*e.g.* see methods in (Caro 1994), (Kruuk 1972) or (Schaller 1972b)). For this study, a compromise was made by visiting each of a set of randomly chosen point transect stations in each study area every month as well as many non-random scanning points chosen for their good visibility during an exploratory period at the start of the study, or already used by the Serengeti Cheetah Project (S. Durant, *pers. comm.)*. The random points therefore ensured a roughly even coverage of all three study sites and avoided assumptions of where to look for predators having been placed using a random number generator and a 1:50000 map of the study regions, whilst use of non-random points maximised the number of sightings made.

Cheetahs were identified using coat spot patterns which are unique to each individual (Caro & Durant 1991) and provide a ready means of identification visible from long distances. Once a cheetah was sighted it was immediately photographed using either a 400mm or 600mm mirror lens, capturing several different angles and ideally including both flanks perpendicular to the lens. Identification was then carried out either in the field or from photographs using areas of the coat with a distinctive pattern, such as merged spots, particularly large or small spots or distinctive patterns. Sightings were then compared to an existing database of recognised individuals in the Serengeti. Once three or more regions of spots had been matched with a previous record, sightings were considered matched. If a matching was not found in existing records a new record was created. Databases for the Loliondo Game Controlled Area and Ngorongoro Conservation Area were created in this way.

Statistical analysis

Call-ins

The primary aim of the analysis was to determine the difference between responses to call-ins for each species in each of the three study regions. However, variation in responses could be confounded by many other factors. To account for this, multivariate analysis was carried out upon each of the four main carnivores to respond to call-ins (lions, spotted hyaenas, black backed and golden jackals). All were represented in all three study regions. Since the response data were not normal (using a one sample Kolmogorov-Smirnov test: black backed jackals, K.S. =2.93, N.S. golden jackals, K.S. =2.15, N.S., hyaena z=5.87, N.S., lions z=5.43, N.S.) and consisted of clumped count data with many zeros, generalised linear models (GLM) were used (Crawley 1993). However, since the data were recorded at repeated, nested levels (due to the repeat surveying of each call-in site) an Iterative Residual

Maximum Likelihood model (IRREML) was used for analysis. IRREMLs are a form of Generalised Linear Mixed Model, allowing specification of non-normal error structures as in GLMs but also allowing nested, random variables to be fitted. Random variables take into account levels of data that are repeatedly sampled such as the year, season or call-in site as opposed to the fixed variables that describe the effects being investigated. In this case only the call-in station was used as the random variable since the effects of year and season were required in the results. All likely explanatory parameters were then added to the model as fixed variables with the relevant interactions (the maximal model), excluding those correlated with other variables. For a list of all variables used, see Table 13. The model was then reduced sequentially, using Wald statistics (which have a χ^2 distribution) to calculate the explanatory power of each of the terms and to remove the least significant. This process was continued until all remaining terms explained a significant proportion of the model deviance (the minimal model). Statistics and probability values are presented for all model terms and interactions. For significant terms these represent the probability values within the minimal model (for individual components of interactions these represent the significance with the interactions removed). For non-significant terms these values are obtained by adding the term to the minimal model and recording the change in deviance. Significant terms are also presented as the minimal model, showing the average effect and standard error of each level after setting the first level (numerically or alphabetically) to 0. The effects of different levels within a term were investigated by re-running the model with a restriction on a single level. For example, the individual effects of the three regions were analysed by restricting one region and running the analysis with just two.

The call-in responses were analysed at two levels. Firstly, a simple presence or absence of each species at every call-in was analysed using an IRREML specifying a binomial error structure appropriate for presence / absence data and the logit link (Crawley 1993). Secondly the actual number of responses for each species was analysed using an IRREML specifying Poisson errors appropriate for count data but corrected for over-dispersion (McCullagh & Nelder 1989) and the log link function (Crawley 1993).

Table 13 – Potentially explanatory factors used in the IRREML analysis.

Model term	Description
Random term:	
Call-in station	Each call-in station was given a unique label.
Fixed terms:	
Hyaena presence	The presence / absence or total number of hyaenas present at a call-in was recorded to assess the impact on other species
Lion presence	The presence / absence or total number of lions present at a call-in was recorded to assess the impact on other species
Livestock levels	Livestock levels were measured on the same strip transects as prey and included counts for cattle, sheep, goats and donkeys. Counts of people were highly correlated with livestock therefore only livestock was used as a measure of human presence. Average livestock per km^2 were transformed to give the closest to normal distribution by adding 1 and logging*.
Prey levels	Prey levels were measured within one week either side of the call-in on 5000x400m strip transects within the 5 km^2 surrounding the call-in station. Most call-ins were supported by 2-3 strip transects. All species considered potential prey were counted (herbivores larger than a hare – a range of fourteen species) but counts of carnivores, people or livestock were excluded. The average number of prey per km^2 was then transformed to a roughly normal distribution before addition to the model by adding one (since many values were zero) and logging*.
Region	Region described the study area and had three levels: Loliondo, Ngorongoro and Serengeti. Region could have acted as a higher random term but was kept as a fixed term as its effect was one of the primary interests.
Season	Seasons were classified at four levels; Start of the dry (July), End of the dry (October), Short wet (January) and Long wet (April).
Temperature	The temperature in degrees Celsius was recorded at the start and end of every call-in outside the car and the mean used in the analysis. Temperature was chosen in preference to call-in start time with which there was high correlation.
Wind speed	Wind speed was measured at the start and end of every call-in metres per second using an anemometer and the mean used in the analysis.
Year	Year 1 referred to the first year of surveying (July 99-April 00), year 2 to the second year (July 00-April 01).
Interactions	
Region*Season	The interaction between region and season was used to see show whether seasonal variation was constant across each of the study areas
Region*Year	The interaction between region and year showed whether yearly differences were

Model term	Description
	constant throughout all regions
Year*Season	The interaction between year and season was used to show whether seasonal differences were constant between years.

***Although not essential it is advised to transform data to closer to normal before entry into the model (Crawley 1993).**

Individual recognition

Unfortunately, re-sighting rates of individually recognised cheetahs were not high enough for rigorous mark-recapture analysis, and many of the assumptions of mark recapture models could not be met (see (Cooper & Durant In press) for a discussion of the problems of applying mark-recapture to cheetah populations). Therefore, cheetahs were analysed by calculating the minimum number of individuals present by matching all sightings of the same cheetah (*e.g.* see (Maddock & Mills 1994) for a similar analysis using wild dogs).

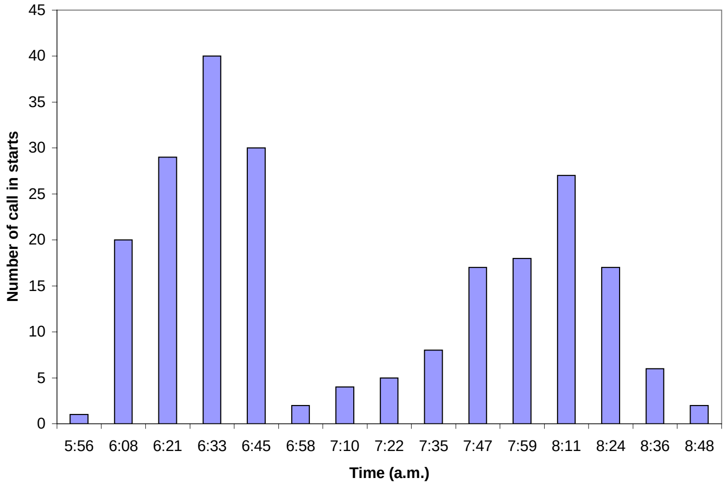
Survey effort

221 call-ins were completed with complementary transects to measure prey. 105 of these were carried out in Loliondo in 8 surveys (July 99 – April 01), 70 in the Serengeti over 7 surveys (October 99 – April 01) and 47 in Ngorongoro over 4 surveys (July 00 – April 01) (see Table 14). The survey of Loliondo was conducted over two years starting in July 1999, the Serengeti survey starting in October 1999 and the census of Ngorongoro conducted over one year starting in July 2000. All call-ins were started before 9 a.m. Most early call-ins started around 06:30 and most second call-ins at 08:00 (see Figure 13).

Table 14 – Summary of call-ins used for main analysis

Survey	Date	Loliondo	Ngorongoro	Serengeti	Total
			Number of call-ins		
1	July 99	4	0	0	4
2	October 99	14	0	10	24
3	Jan 00	15	0	10	25
4	April 00	10	0	10	20
5	July 00	11	12	10	33
6	October 00	17	12	10	39
7	January 01	15	11	10	36
8	April 01	18	12	10	40
Grand Total		104	47	70	221

Figure 13- Distribution of call-in start times



4.4 Results

Call-in responses

Response diversity

A total of 21 different species responded to the call-ins, 14 of which were birds. Loliondo displayed the highest diversity of species responses (19 species with a mean of 0.18 per call-in) and was the only region where striped hyaenas were recorded. Serengeti had the second highest diversity (12 species, mean 0.17 per call-in) and was the only region where side striped jackals were recorded. Ngorongoro had 11 species (mean 0.15 per call-in) and no unique species (see Table 15).

Table 15 - Species responding to all call-ins carried out (n=232)

Species	Region			
	Loliondo	Ngorongoro	Serengeti	All areas
Mammals				
Black backed jackal (*Canis mesomelas*)	168	16	21	205
Golden jackal (*Canis aureus)*	40	34	16	90
Side striped jackal (*Canis adustrus*)	0	0	3	3
Hyaena (*Crocuta crocuta*)	526	324	691	1541
Striped hyaena (*Hyaena hyaena*)	3	0	0	3
Lion (*Panthera leo*)	114	28	52	194
Man (*Home sapien*)	39	6	0	45
Birds				
Auger buzzard (*Buteo auger*)	3	0	0	3
Bataleur (*Terathopius ecaudatus*)	5	0	3	8
Fish Eagle (*Haliaetus vocifer*)	1	0	0	1
Griffon vulture (*Gyps rueppellii*)	3	0	0	3
Hooded vulture (*Necrosyrtes monachus*)	26	27	23	76
Black kite (*Milvus migrans*)	1	0	0	1
Lappet faced vulture (*Aegypius tracheliotus)*	35	3	14	52
Maribou stork (*Leptoptilos crumeniferus*)	3	7	0	10
Martial eagle (*Hieraaetus bellicosus*)	0	0	1	1

Species	Region			
Pied crow (*Corvus albus*)	26	0	0	26
Tawney / Steppe eagle (*Aquila rapax*)	38	13	6	55
White backed vulture (*Gyps africanus*)	81	10	14	105
White headed vulture (*Aegypius occipitalis*)	5	2	1	8
Total species responding	18	11	12	20
Total responses	1117	470	845	2432

Further analysis was restricted to the four main responding species; black-backed and golden jackals, spotted hyaenas and lions and to the 221 call-ins with complimentary prey data. Spotted hyaenas were present in the highest numbers, responding to roughly 80% of call-ins in all regions with up to 47 individuals at a single call-in. Black backed jackals were the second most common, responding to between 17 and 59% of call-ins depending on the region, followed by lions that responded to an average of 22% of call-ins and were generally the slowest to arrive. A summary of the response patterns is shown in Table 16.

Table 16 – Summary of response patterns of main carnivores

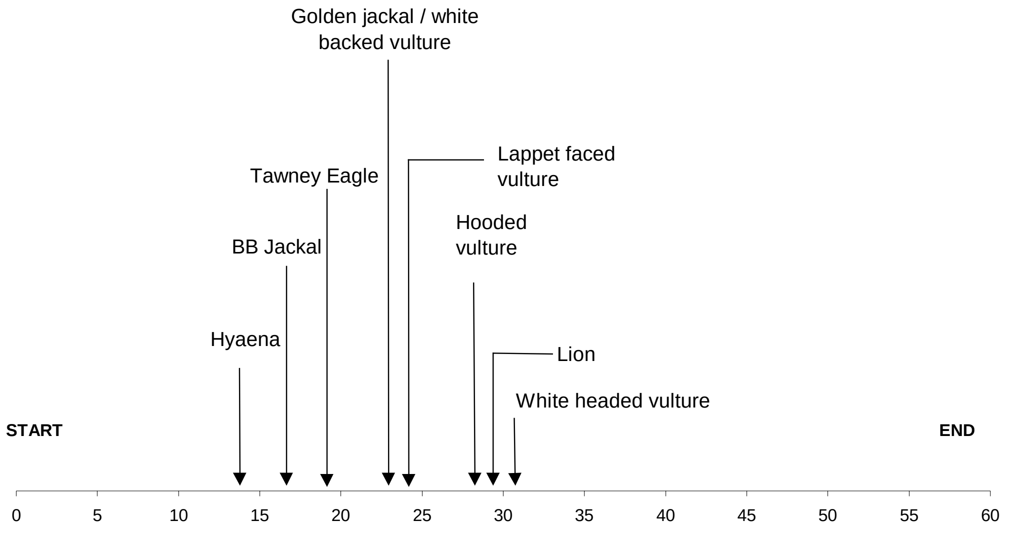
		Loliondo	NCA	SNP	Total
Black backed jackal	No. call-ins	104	47	70	221
	% call-ins with at least one response	59	23	17	38
	Mean responses per call-in (±SE)	1.5(±0.2)	0.3(±0.1)	0.3(±0.1)	0.9(±0.1)
	Max. no. responses at one call-in	8	3	3	8
	Total responses	153	16	21	190
Golden jackal	No. call-ins	104	47	70	221
	% call-ins with at least one response	20.2	27.7	8.6	18.1
	Mean responses per call-in (±SE)	0.4(±).1)	0.7(±0.2)	0.2(±0.1)	0.4(±0.1)
	Max. no. responses at one call-in	5	7	9	9
	Total responses	37	34	16	87
Hyaena	No. call-ins	104	47	70	221
	% call-ins with at least one response	77.9	85.1	84.3	81.4

		Loliondo	NCA	SNP	Total
	Mean responses per call-in (±SE)	4.8(±0.6)	6.9(±1.1)	9.9(±1.4)	6.8(±0.6)
	Max. no. responses at one call-in	35	34	47	47
	Total responses	499	324	678	1501
Lion	No. call-ins	104	47	70	221
	% call-ins with at least one response	26	12.8	21.4	21.7
	Mean responses per call-in (±SE)	1.0(±0.2)	0.6(±0.3)	0.8(±0.2)	0.9(±0.1)
	Max. no. responses at one call-in	13	8	8	13
	Total responses	108	27	52	187

Response patterns

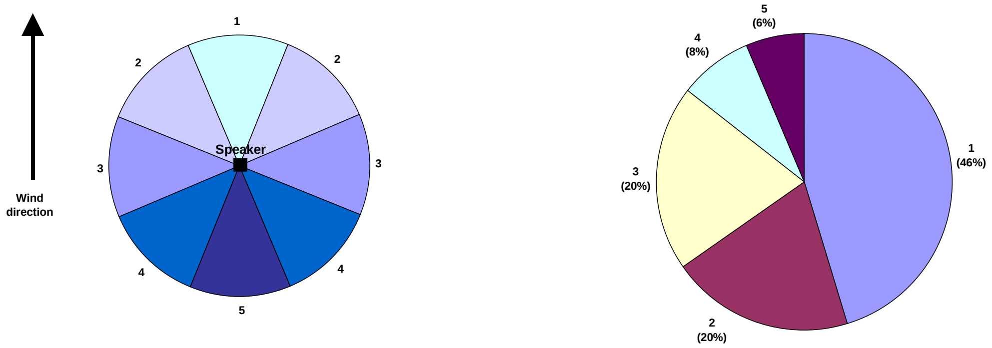
Most species responded on average between 15 and 30 minutes of the start of the tape with lions being on of the slowest species to respond (Figure 14), suggesting that one hour was a sufficient time to wait at a call-in.

Figure 14 - Schematic representation of mean earliest arrival times for various species responding to call-ins.



The direction of approaches to the call-ins was not random. By assigning the approach direction of each response to one of five categories based upon the eight compass points it can be seen that a large majority of the major carnivores responding approached from the direction of the wind (see Figure 15). The differences between the observed approaches were highly significantly different from random (hyaenas: χ^2_4= 639.2, n=1216, lions: χ^2_4= 68.7 n=158, black backed jackals: χ^2_4= 91.8, n=158, golden jackals χ^2_4= n=67; p<0.001 for all species) with all showing over 50% responses within directions 1 and 2. The only exception was the approach direction of Maasai who also occasionally responded to the call-in. Although their approach was significantly different from random (χ^2_4=37.2, p<0.001, n=39), 64% approached from direction 3, at right angles to the wind direction. See Appendix III for further analysis of response patterns.

Figure 15 – Division of response directions in relation to the wind. The left chart shows the division of responses in relation to wind direction. The right chart shows the combined percentages of black backed jackals (n=158), golden jackals (n=67), spotted hyaenas (n=1216) and lions (n=158) responding to call-ins at each of these eight directions.



Response analysis

Black backed jackals

Presence / absence

Modelling the effect of potential explanatory variables on the presence or absence of black backed jackals showed that responses varied significantly with year, season, region and temperature (see Table 17). Responses were significantly more likely in Loliondo than the Serengeti (χ^2_1=16.35, p<0.001) but not significantly higher than Ngorongoro (χ^2_1=2.79, p=0.095). Insufficient data were available to compare the Serengeti and Ngorongoro. Chance of response also varied temporally, with significantly more call-ins in the first year and in the dry season attracting a response. Responses were less likely with increasing temperature. Neither seasonal nor yearly variation differed between regions and seasonal variation was also constant between years. The chance of a response was unaffected by the local prey or livestock presence, wind or whether or not lions or hyaenas responded to the same call-in.

Table 17 – IRREML analysis of factors affecting presence or absence of black backed jackals at call-ins. The lower part of the table shows the minimal model, comprised of only significant individual terms, together with their average effect on the response variate. The effect of the random term is shown below the table.

Model term	Wald statistic (χ^2)	Degrees of freedom	P
Year	27.07	1	0.000
Region	21.91	2	0.000
Temperature	9.94	1	0.002
Season	11.6	3	0.009
Lions	2.52	1	0.112
Wind	2.44	1	0.118
Livestock	1.81	1	0.179
Hyaenas	1.54	1	0.215
Prey	0.58	1	0.446
Region*Year	1.33	3	0.167
Year*Season	0.29	3	0.962
Region*Season	5.07	6	1.000
Minimal model		Average effect	Standard error
Constant		0.47	1.04
Year	1	0.00	0.00
	2	-2.26	0.43
Season	Dry end	0.00	0.00
	Dry start	0.83	0.50
	Long wet	-0.29	0.45
	Short wet	-0.97	0.47
Region	Loliondo	0.00	0.00
	Ngorongoro	-0.83	0.50
	Serengeti	-2.40	0.52
Temperature		-0.11	0.03

Call-in station, 0.52 ± 0.39

Number of responses

Analysis of the numbers of black backed jackals responding to each call-in showed similar results to the analysis of presence / absence (Table 18). More responses occurred to call-ins in Loliondo than in the Serengeti (χ^2_1= 20.54, p<0.001) and Ngorongoro (χ^2_1=4, p=0.045) and responses were also significantly higher in

Ngorongoro than the Serengeti (χ^2_1=4.24, p=0.039). Responses were higher in the first year, with no difference in region, and they decreased with increasing temperature. However, no significant difference was seen in the number of jackals responding between seasons, either overall or within any region, despite the previous analysis showing the *chance* of a response being higher during the dry seasons. This suggests that although responses were rarer they consisted of more animals in the wet season. Graphic representations of regional and temporal effects on black backed jackals controlling for all other factors in the minimal model are given in Figure 16 and Figure 17.

Table 18 - IRREML analysis of factors affecting the number of black backed jackal numbers responding to call-ins. The effect of the random term is shown below the table.

Model term	Wald statistic (χ^2)	Degrees of freedom	P
Year	25.32	1	0.000
Region	24.11	2	0.000
Temperature	14.04	1	0.000
Hyaenas	2.56	1	0.110
Lions	2.45	1	0.118
Prey	1.27	1	0.260
Season	2.15	3	0.542
Wind	0.13	1	0.718
Livestock	0.02	1	0.888
Interval	0.00	1	0.974
Region*Season	10.84	9	0.287
Region*Year	0.30	1	0.584
Year*Season	2.82	5	0.728
		Average effect	Standard error
Constant		2.68	0.486
Year	1	0.00	0.000
	2	-1.06	0.211
Region	Loliondo	0.00	0.000
	Ngorongoro	-0.70	0.363
	Serengeti	-1.79	0.382
Temperature		-0.08	0.020

Call-in station, 0.00 ± 0.08

Figure 16 - IRREML predictions for the effect of region on the average number of black backed jackals responding to call-ins. Bars denote standard errors.

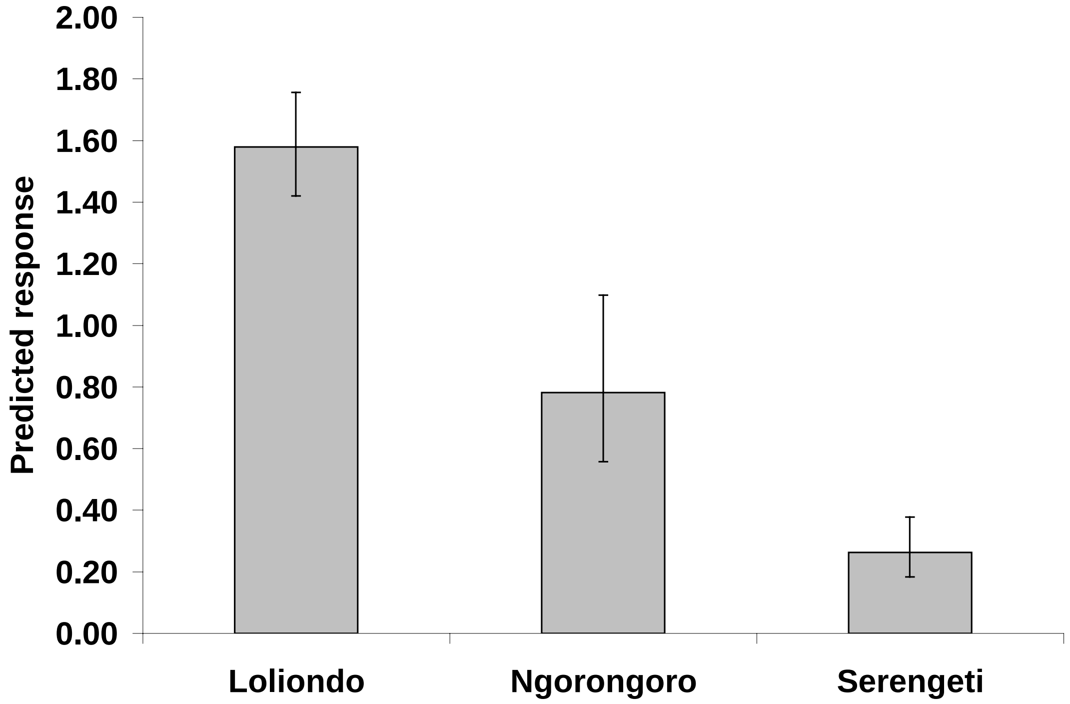
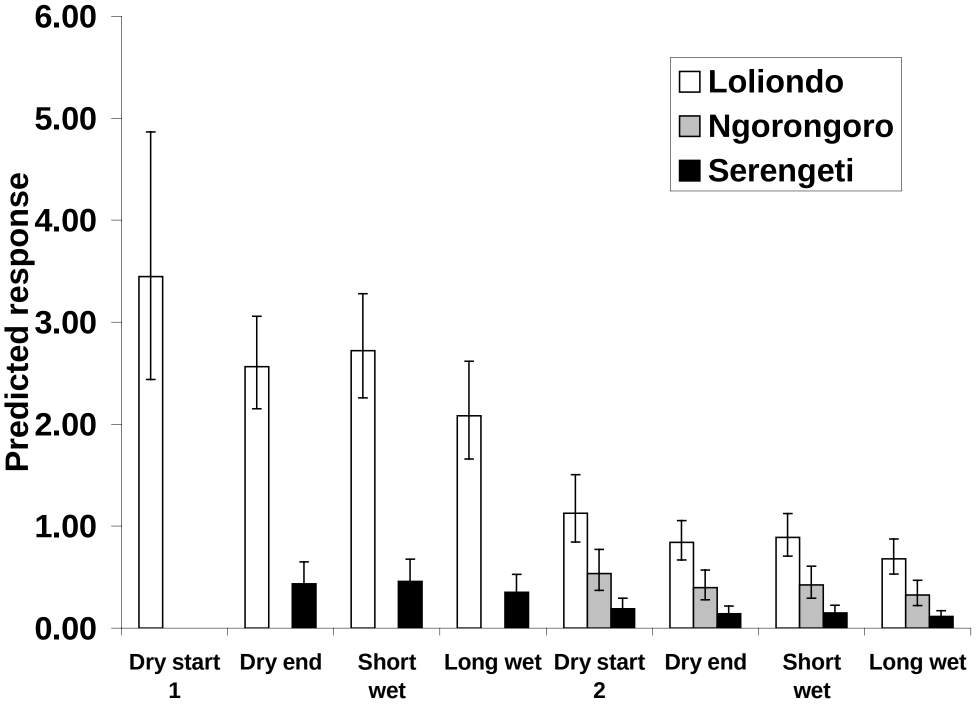


Figure 17 - IRREML predictions for the effect of year, season and region on the average number of black backed jackals responding to call-ins. Bars denote standard errors.



Golden jackals

Presence / absence

Golden jackal responses varied significantly by region with responses in Ngorongoro significantly more likely than in the Serengeti ($\chi^2_1=4.51$, p=0.034) or Loliondo ($\chi^2_1=5.65$, p=0.017), but no difference between the Serengeti and Loliondo ($\chi^2_1=1.71$, p=0.191). Chance of response also varied temporally, both within and between regions and years. Seasonal variation was different in each region, with responses most likely in Ngorongoro and the Serengeti at the start of the dry season, but most likely in Loliondo in the short wet season. Responses in the wet season were higher in the second year. Golden jackal responses were also affected negatively by temperature and by other species. A response was *more* likely in areas with high livestock numbers and at call-ins where a hyaena also responded but less likely at call-ins where lions responded (Table 19).

Table 19– IRREML analysis of factors affecting golden jackal presence or absence at call-ins. The lower part of the table shows the minimal model, comprised of only significant individual terms, together with their average effect on the response variate. The effect of the random term is shown below the table.

Model term	Wald statistic (χ^2)	Degrees of freedom	P
Year	32.9	1	0.000
Season	38.9	3	0.000
Region	9.25	2	0.010
Temperature	4.05	1	0.044
Wind	0.11	1	0.740
Prey	1.86	1	0.173
Livestock	10	1	0.002
Hyaenas	22.77	1	0.000
Lions	37.71	1	0.000
Region*Year	4.48	1	0.000
Region*Season	62.39	6	0.000
Year*Season	35.14	2	0.000
		Average effect	Standard error
Constant		0.47	1.04
Year	1	0.00	0.00
	2	-3.37	0.59
Season	Dry end	0.00	0.00
	Dry start	3.65	0.71

Model term	Wald statistic (χ^2)	Degrees of freedom	P
	Long wet	-0.09	0.56
	Short wet	-0.44	0.62
Region	Loliondo	0.00	0.00
	Ngorongoro	2.03	0.95
	Serengeti	-1.36	1.05
Temperature		-0.08	0.05
Livestock		0.37	0.20
Hyaena presence		1.40	0.69
Lion presence		-1.70	0.57

Call-in station, 4.17 ± 1.39

Number of responses

Variation of the number of golden jackals responding to call-ins was explained significantly by the region, year and season (Table 20). Most golden jackals responded in Ngorongoro, significantly more than the Serengeti (χ^2_1=10.28, p=0.001) or Loliondo (χ^2_1=9.84, p=0.002). Differences between the Serengeti and Loliondo were insignificant (χ^2_1=0.79, p=0.373). Responses were also higher in the first year and varied seasonally. However, seasonal changes were significantly different in each region and year. Responses were highest in the Serengeti and Loliondo at the end of the dry season in the first year but at the beginning of the dry in the second year when responses were highest in Ngorongoro were extremely high during the second dry season but low for the rest of the year. The numbers responding were not significantly affected by other species or environmental conditions. Graphic representations of regional and temporal effects on black backed jackals controlling for all other factors in the minimal model are given in Figure 18 and Figure 19.

Table 20– Factors affecting the number of golden jackals responding to call-ins. The lower part of the table shows the minimal model, comprised of only significant individual terms, together with their average effect on the response variate. The effect of the random term is shown below the table.

Model term	Wald statistic (χ^2)	Degrees of freedom	P
Year	62.69	1	0.000
Season	79.19	3	0.000
Region	12.36	2	0.002
Lions	2.26	1	0.133
Interval	1.91	1	0.167
Temperature	1.25	1	0.264
Wind	1.21	1	0.271
Hyaenas	1.03	1	0.310
Prey	0.60	1	0.438
Livestock	0.05	1	0.827
Year*Season	10.79	3	0.013
Region*Season	13.64	6	0.034
Region*Year	0.59	1	0.442
		Average effect	Standard error
Constant		-0.68	0.41
Year	1	0.00	0.00
	2	-2.57	0.32
Season	Dry end	0.00	0.00
	Dry start	1.47	0.27
	Long wet	-1.20	0.30
	Short wet	-1.13	0.31
Region	Loliondo	0.00	0.00
	Ngorongoro	2.02	0.67
	Serengeti	-0.60	0.74

Call-in station, 2.54 ± 0.76

Figure 18 – The effect of region on the average number of golden jackals responding to call-ins, controlling for all other significant factors in the minimal model. Bars denote standard errors.

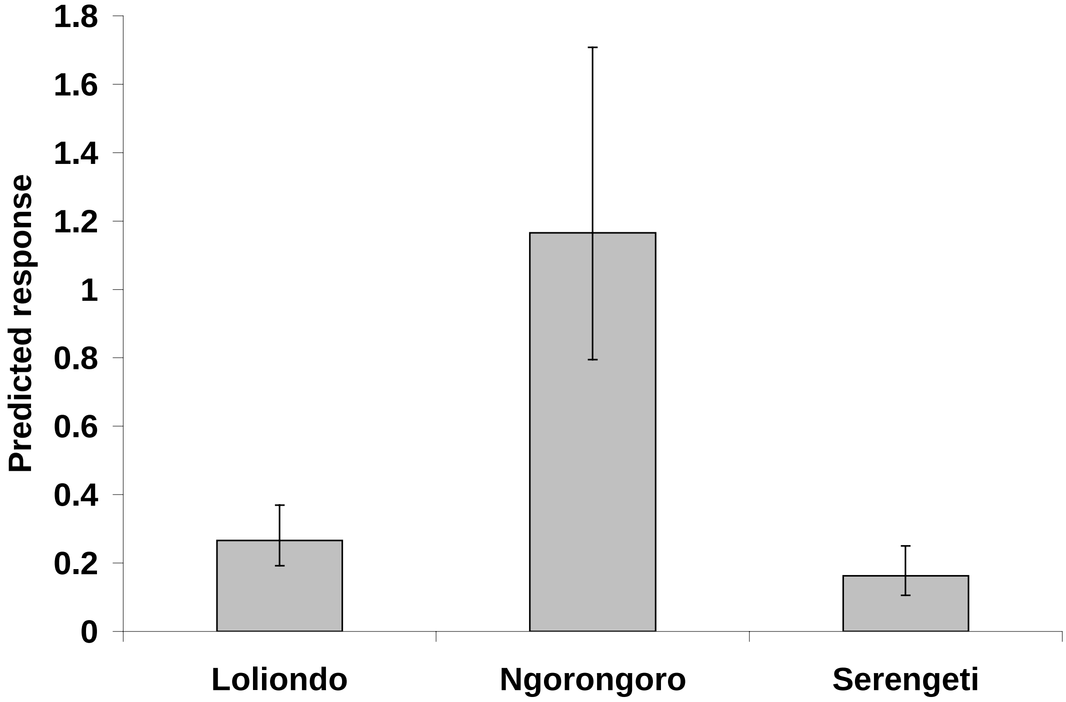
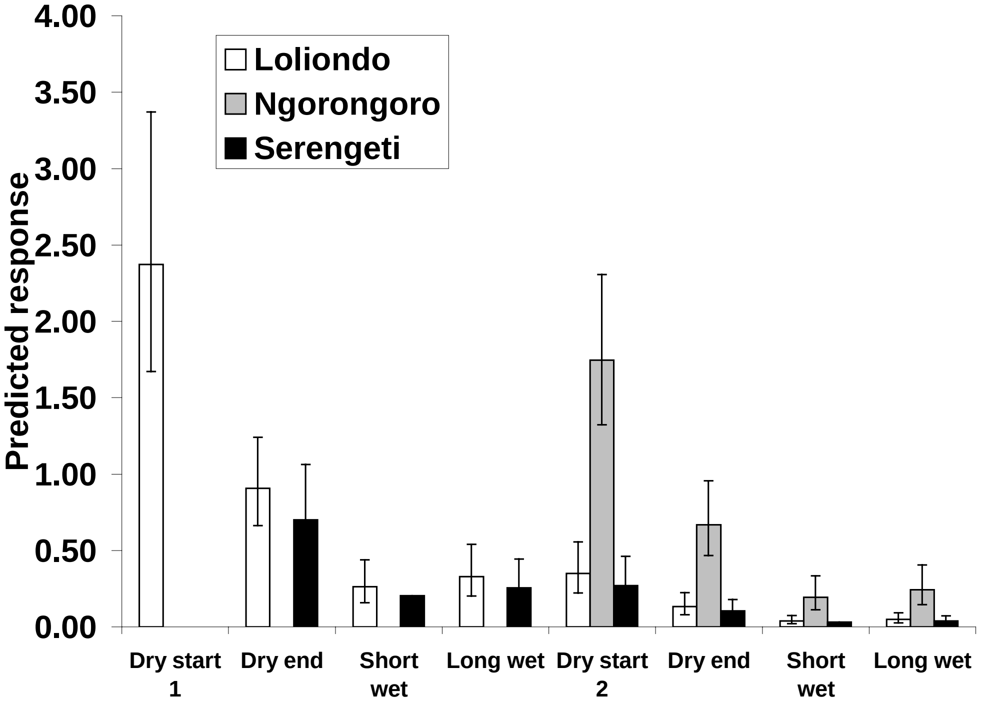


Figure 19 - Predictions for the effect of year, season and region on the average number of golden jackals responding to call-ins, controlling for all other significant factors in the minimal model. Bars denote standard errors.



Spotted hyaenas

Presence / absence

Hyaena presence at call-ins was significantly affected by the year, season and prey levels but not by region (Table 21). Responses were equally likely in each region. Responses were again less likely in the second year and, controlling for region, responses were most likely at the beginning of the dry season and least likely at the end. (Insufficient data were available to analyse the interaction between region and season). Hyaenas were present at call-ins more often when prey levels were higher.

Table 21 – IRREML analysis of factors affecting spotted hyaena presence or absence at call-ins. The lower part of the table shows the minimal model, comprised of only significant individual terms, together with their average effect on the response variate. The effect of the random terms is shown below the table.

Model term	Wald statistic (χ^2)	Degrees of freedom	P
Year	9.11	1	0.003
Season	12.97	3	0.005
Region	1.49	2	0.475
Temperature	0.52	1	0.471
Wind	1.17	1	0.279
Prey	6.18	1	0.013
Livestock	2.97	1	0.085
Lions	0.47	1	0.493
Year*Season	6.06	3	0.109
Region*Year	2.52	3	0.472
Minimal model		Average effect	Standard error
Constant		1.28	0.60
Year	1	0.00	0.00
	2	-1.16	0.39
Season	Dry end	0.00	0.00
	Dry start	1.73	0.53
	Long wet	0.20	0.39
	Short wet	0.87	0.42
Prey		0.34	0.14

Call-in station, 3.45 ± 1.06

Number of responses

Analysis of hyaena responses shows that the year, region, season, temperature and wind all had a significant effect (Table 22). Although the chance of a response was equal in all areas, the number of responses was highest in Ngorongoro and the Serengeti and significantly lower in Loliondo (vs. Serengeti χ^2_1=16.69, p<0.001, vs. Ngorongoro χ^2_1=6.29, p=0.012). Variation also occurred across year and season to different degrees in each region. In the Serengeti and Ngorongoro responses were generally higher in the dry seasons, whereas responses were generally more stable across seasons in Loliondo with a slight dip at the end of the dry season of each year. Responses were lower in the second year for all areas but differences were greatest for the Serengeti. Hyaena responses were also significantly lower in higher temperatures or wind speeds but increased with local prey concentrations. Graphic representations of regional and temporal effects on spotted hyaenas, controlling for all other factors in the minimal model, are given in Figure 20 and Figure 21.

Table 22 – IRREML analysis of numbers of spotted hyaenas arriving at call-ins. The lower part of the table shows the minimal model, comprised of only significant individual terms, together with their average effect on the response variate. The effect of the random term is shown below the table.

Model term	Wald statistic (χ^2)	Degrees of freedom	P
Year	46.45	1	0.000
Season	12.77	3	0.000
Region	19.69	2	0.002
Temperature	14.98	1	0.000
Wind	23.07	1	0.000
Prey	10.11	1	0.001
Livestock	0.98	1	0.322
Lions	0.17	1	0.680
Region*Year	7.32	1	0.007
Region*Season	16.86	6	0.010
Year*Season	12.02	6	0.062
		Effect	Standard error
Constant		3.05	0.40
Year	1	0.00	0.00
	2	-1.02	0.15
Region	Loliondo	0.00	0.00
	Ngorongoro	0.83	0.24

Model term	Wald statistic (χ^2)	Degrees of freedom	P
	Serengeti	0.82	0.21
Season	Dry end	0.00	0.00
	Dry start	0.59	0.22
	Long wet	-0.16	0.18
	Short wet	-0.01	0.17
Temperature		-0.05	0.01
Wind		-0.14	0.03
Prey		0.22	0.05

Call-in station, 0.159 ± 0.075

Figure 20 - IRREML predictions for the effect of region on the average number of spotted hyaenas responding to call-ins, controlling for all other significant factors in the minimal model. Bars denote standard errors.

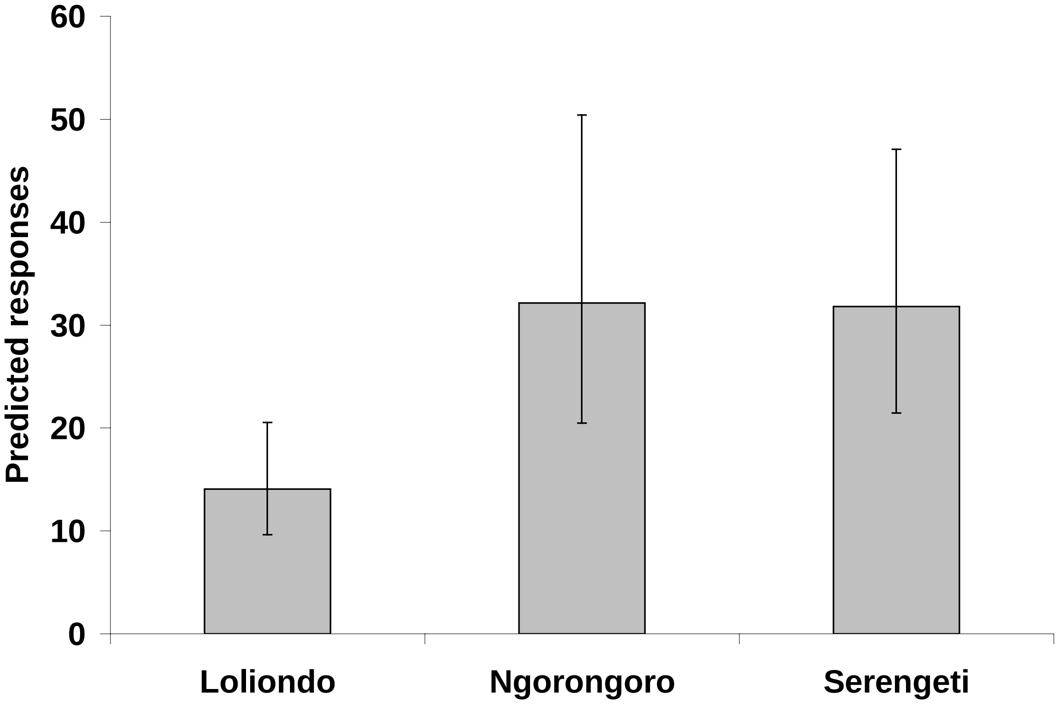
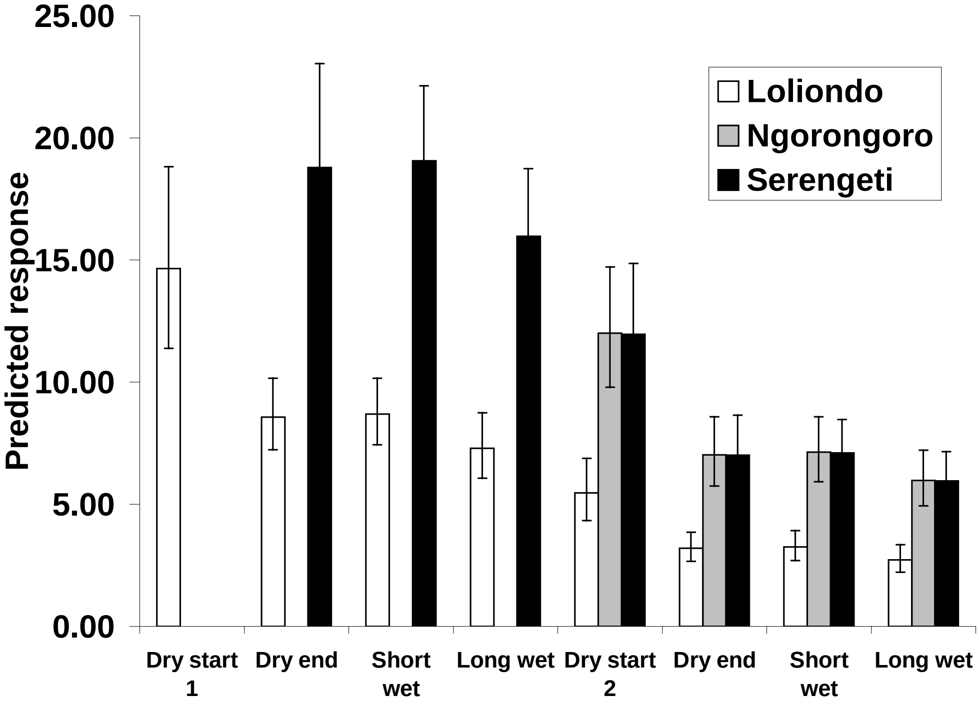


Figure 21 - Predictions for the effect of year, season and region on the average number of spotted hyaenas responding to call-ins, controlling for all other significant factors in the minimal model. Bars denote standard errors.



Lions

Presence / absence

Like hyaenas, there were no differences in the presence or absence of lions at call-ins between each of the three regions. Presence was affected by year, being less likely in the second year, and by season, with most present at the beginning of the dry season and fewest in the wet. Yearly differences were the same in all regions and seasonal differences were the same in each year, however, the interaction between region and season could not be tested (

Table 23).

Table 23 – IRREML analysis of lion presence or absence at call-ins. The lower part of the table shows the minimal model, comprised of only significant individual terms, together with their average effect on the response variate. The effect of the random term is shown below the table.

Model term	Wald statistic (χ^2)	Degrees of freedom	P
Year	13.89	1	0.000
Season	15.41	3	0.001
Region	1.33	2	0.514
Temperature	0.33	1	0.566
Wind	2.75	1	0.097
Prey	2.7	1	0.100
Livestock	3.21	1	0.073
Hyaenas	0.87	1	0.351
Year*Season	1.75	3	0.626
Region*Year	2.99	3	0.393
Minimal model		Average effect	Standard error
Constant		-0.47	0.36
Year	1	0.00	0.00
	2	-1.31	0.35
Season	Dry end	0.00	0.00
	Dry start	1.07	0.45
	Long wet	-0.61	0.43
	Short wet	-0.66	0.42

Call-in station, 0.94 ± 0.46

Number of responses

The number of lions responding to call-ins varied with year and season, but not region (

Table 24). The greatest numbers responded in the dry season and the lowest numbers responded in the long wet season with the same patterns exhibited in all three regions across both years. However, as with the other species studied, responses were lower in the second year. Graphic representations of regional and temporal effects on lions, controlling for all other factors in the minimal model, are given in Figure 22 and Figure 23.

Table 24 - IRREML analysis of numbers of lions responding to call-ins. The lower part of the table shows the minimal model, comprised of only significant individual terms, together with their average effect on the response variate. The effect of the random term is shown below the table.

Model term	Wald statistic (χ^2)	Degrees of freedom	P
Year	14.56	1	0.000
Season	16.7	3	0.001
Interval	5.56	1	0.018
Livestock	3.16	1	0.075
Prey	1.94	1	0.164
Wind	1.54	1	0.215
Temperature	0.61	1	0.435
Hyaenas	0.12	1	0.729
Region	0.43	2	0.807
Region*Year	4.58	3	0.205
Year*Season	0.63	3	0.890
Region*Season	3.26	8	0.917
Minimal model		Average effect	Standard error
Constant		0.49	0.26
Year	1	0.00	0.00
	2	-1.04	0.27
Season	Dry end	0.00	0.00
	Dry start	0.37	0.34
	Long wet	-0.90	0.33
	Short wet	-0.82	0.31

Call-in station, 0.94 ± 0.37

Figure 22 - IRREML predictions for the effect of region on the average number of lions responding to call-ins, controlling for all other significant factors in the minimal model. Bars denote standard errors.

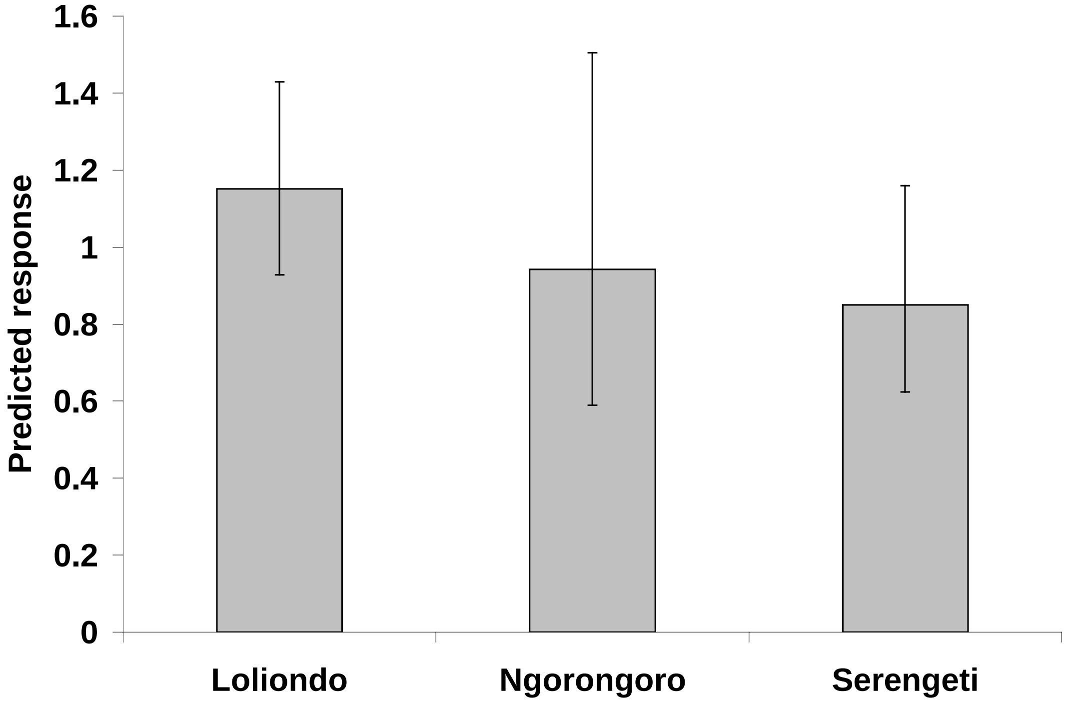
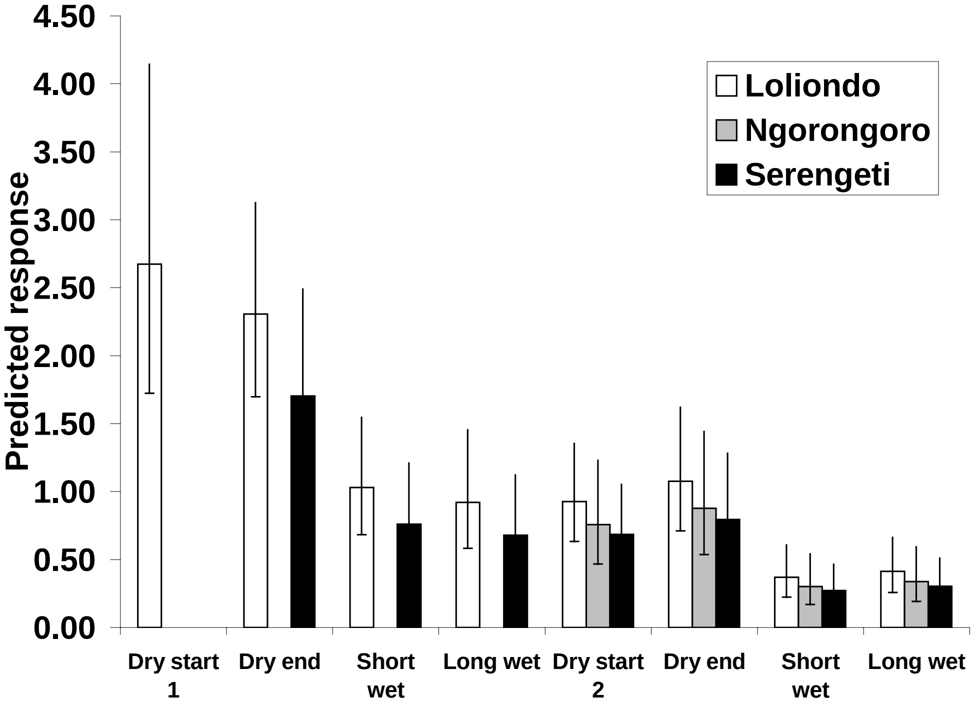


Figure 23 - IRREML predictions for the effect of year, season and region on the average number of lions responding to call-ins, controlling for all other significant factors in the minimal model. Bars denote standard errors.



Call-in population estimates

Calibrations

Determination of the audible range

Response distance

Fifteen calibrations were carried out on lions, covering a total of 73 lions. Lion calibrations were carried out up to 3500m from the call-in speaker. The maximum response distance (indication that the call-in was heard) or arrival distance (movement to within sight of the call-in) recorded for lions was 2160m with a medium crosswind. At 2500m with a medium wind toward the lions or above, no response was obtained. Eleven calibrations covering 22 hyaenas were carried out up to a distance of 5200m. The maximum response and arrival distance was 2500m with a medium wind towards the animals. At 2610m with a low crosswind, or 2970 with a strong wind towards the animals, no response was obtained. Responses within the audible range were assumed to be unaffected by distance, as shown by Mills (Mills *et al*. 2001).

Effect of wind

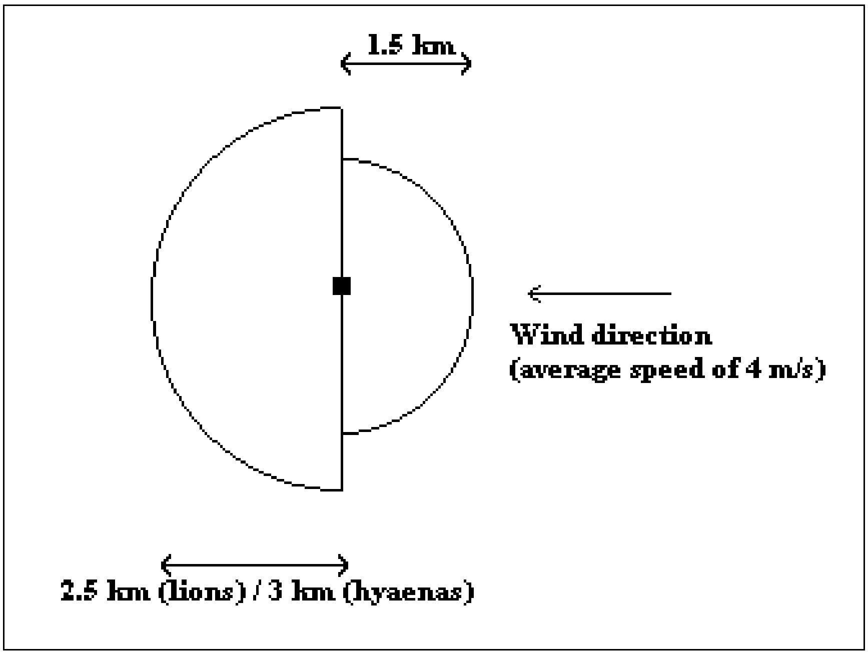
No difference was seen for lions between experiments with the wind towards the subjects and low to medium crosswinds. However, high crosswinds were not tested. The maximum response with the wind blowing away from the subject was just 1000m at medium strength. On a separate occasion a non-response was obtained at 1000m with a high strength wind, however, the subject was then re-tested at a lower distance and still did not respond, suggesting that the non-response was not due to the wind.

Hyaenas did not respond when a low crosswind was present at 2610m or with a high wind away from the subject at 1500m but did respond to all downwind calibrations up to 2500m

Calculation of sampled area

Previous studies have assumed the sampled area to be a circle around the call-in station with a radius equal to the maximum known audible range for a given species (Ogutu & Dublin 1998), (Mills *et al*. 2001). However, since the direction of response to call-ins (Figure 15) and the calibration results show that wind direction had a strong effect, this study has attempted to improve the accuracy of the audible area estimate by calculating an asymmetrical area around the speaker. Using the overall mean wind speed of 4 m/s, the response area for the average call-in was calculated using 2500 m as the audible distance in the direction of the wind for lions and 3000 m for hyaenas and 1500m as the radius against the wind for both species. All values were chosen as slightly above the maximum known radii (see Figure 24). These give an estimated average audible area of 13.4 km^2 per call-in for lions and 17.7 km^2 for hyaenas.

Figure 24 – Estimated audible range for call-ins



Probability of response within the audible range

Effect of sex and age

Within the areas already determined as theoretically audible to lions, and not including cubs in the analysis, 21% of females arrived at the speaker (n=28) and 29% of males (n=7). Due to the difficulty in sexing hyaenas, the effect of sex on responses could not be determined. 16% of adult lions within known audible range arrived at the speaker (n=31), 75% of adolescents (n=4) and 0% of cubs, old or young. For hyaenas 88% of adults responded (n=8) and 0% of cubs (n=2).

Other effects on response

The presence of cubs for both species strongly reduced the chance of response, with only 16% of adult lions responding if cubs were present (n=12). The only two that did respond left other adults with the cubs when they left. Only one calibration was carried out on hyaenas with cubs, but the female with the cubs did not respond. She was the only adult hyaena not to respond within the known audible range. 0% of adult lions on kills responded to call-ins within the audible range (n=9). No calibrations were carried out on feeding hyaenas. Lions did respond when courting, although only two lions (1 courting pair) were tested within the audible range. Of adult lions with a belly size of 3 or larger, 11% (n=27) responded to the call-in. For belly sizes below 3, 50% (n=4) responded. Habitat and prey levels may have had an effect on the distance call-ins were audible, with bushier habitats expected to have a lower audible range. However, insufficient data were available to test this.

Calibration summary

The calibrations allow calculation of the surveyed area and estimations of response chance within this area. Rather than assume equal audibility in all directions the audible range can be adjusted to account for wind, calculating the audible area for lion to be 13.4km^2 and for hyaenas 17.7km^2. Responses within the audible range show that call-ins are not an effective measure of cubs, but can be used to estimate adult populations. The chance of a response for hyaenas was far greater than for lions. Excluding cubs, 88% of hyaenas within the audible range arrived at the call-in within one hour. This is at the upper range of the response proportion estimated by Mills (2001) who calculated a response probability of 0.61 with large confidence limits of 0.32 to 0.84 due to non-independence of responses (Mills *et al*. 2001). In contrast, 23% of adolescent or adult lions arrived at the call-in within an hour. Younger lions may have been more likely to respond than older adults, however, since the sample sizes were so low, all adults will be treated the same. This was a similar result to that found by Ogutu and Dublin (1988) who found a response proportion of 0.26. Lions on kills, or recently fed, were less likely to respond.

Density estimates

Actual numbers of species per call-in were estimated using the mean numbers of each species responding per call-in, controlling for other significant effects (as predicted by the IRREML analysis) and corrected for the proportion predicted not to respond from the calibrations. These were then divided by the estimated area of each call-in to give an estimate of adult density. For jackals, since calibrations were not carried out, the proportion responding and the audible range were assumed to be equal to hyaenas.

Densities were calculated based upon the overall survey average and individually for each survey since temporal variation was important for all species, both seasonally and annually. Black backed jackals densities were highest in Loliondo with particularly high estimates in the first year of about 0.15 individuals per km^2 falling to 0.05/km^2 in the second year. Densities in the Serengeti and Ngorongoro were much lower, fluctuating around 0.05 individuals per km^2. Golden jackal densities were lower than black backed, with Ngorongoro showing the highest average densities although this was largely driven by a particularly high estimate in the second short dry season (0.1 individuals per km^2) with subsequent surveys less than half the first density. Densities in Loliondo were much higher in the first year (over 0.13/km^2) but fell drastically with subsequent surveys. Densities in the Serengeti were low, fluctuating around 0.04 and falling to almost none in the second year. Hyaena densities were highest in the Serengeti and Ngorongoro, averaging about 0.8 individuals per km^2. However, densities in the Serengeti reached 1.2/km^2 in the first year before falling, suggesting densities were actually higher in the Serengeti overall. Densities were also higher in Loliondo in the first year, fluctuating around 0.6/km^2, but falling in the second year to give a low average. Seasonal variation was different each year but tended to be highest in the dry seasons and lowest in the wet. Compared to lions, densities in the Serengeti and Ngorongoro were about roughly equivalent (1 hyaena to 0.4 lions) but lower than lions in Loliondo. Lion densities were equivalent in all areas (See Table 25 and Figure 25 and Figure 26).

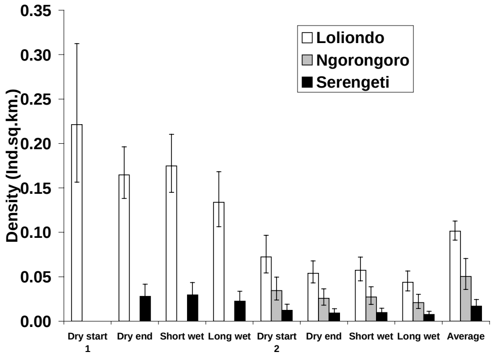
Table 25 - Densities for individual surveys and survey averages. Errors are based on standard errors from IRREML calculations. Insufficient data were available to calculate errors for calibration data.

		Loliondo			Ngorongoro			Serengeti		
Year	Season	Density	SE+	SE-	Density	SE+	SE-	Density	SE+	SE-
Black backed jackals. Response range: 17.7 km. Response proportion: 0.88										
1	Dry start	0.22	0.09	0.06						
	Dry end	0.16	0.03	0.03				0.03	0.01	0.01
	Short wet	0.17	0.04	0.03				0.03	0.01	0.01
	Long wet	0.13	0.03	0.03				0.02	0.01	0.01
2	Dry start	0.07	0.02	0.02	0.03	0.02	0.01	0.01	0.01	0.00
	Dry end	0.05	0.01	0.01	0.03	0.01	0.01	0.01	0.00	0.00
	Short wet	0.06	0.01	0.01	0.03	0.01	0.01	0.01	0.00	0.00

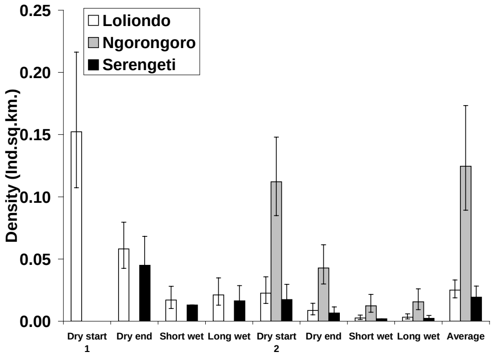
		Loliondo			Ngorongoro			Serengeti		
	Long wet	0.04	0.01	0.01	0.02	0.01	0.01	0.01	0.00	0.00
	Average	0.10	0.01	0.01	0.05	0.02	0.01	0.02	0.01	0.01
Golden jackals. Response range: 17.7 km. Response proportion: 0.88										
1	Dry start	0.15	0.06	0.05						
	Dry end	0.06	0.02	0.02				0.04	0.02	0.02
	Short wet	0.02	0.01	0.01				0.01	0.00	0.01
	Long wet	0.02	0.01	0.01				0.02	0.01	0.01
2	Dry start	0.02	0.01	0.01	0.11	0.04	0.03	0.02	0.01	0.01
	Dry end	0.01	0.01	0.00	0.04	0.02	0.01	0.01	0.00	0.00
	Short wet	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.00	0.00
	Long wet	0.00	0.00	0.00	0.02	0.01	0.01	0.00	0.00	0.00
	Average	0.02	0.01	0.01	0.12	0.05	0.04	0.02	0.01	0.01
Spotted hyaenas. Response range: 17.7 km. Response proportion: 0.88										
1	Dry start	0.94	0.27	0.21						
	Dry end	0.55	0.10	0.09				1.21	0.27	0.22
	Short wet	0.56	0.09	0.08				1.22	0.20	0.17
	Long wet	0.47	0.09	0.08				1.03	0.18	0.15
2	Dry start	0.35	0.09	0.07	0.77	0.17	0.14	0.77	0.19	0.15
	Dry end	0.21	0.04	0.03	0.45	0.10	0.08	0.45	0.11	0.09
	Short wet	0.21	0.04	0.04	0.46	0.09	0.08	0.46	0.09	0.07
	Long wet	0.17	0.04	0.03	0.38	0.08	0.07	0.38	0.08	0.06
	Average	0.34	0.04	0.04	0.74	0.13	0.11	0.74	0.09	0.08
Lions. Response range: 13.4 km. Response proportion: 0.23										
1	Dry start	0.87	0.48	0.31						
	Dry end	0.75	0.27	0.20				0.55	0.25	0.17
	Short wet	0.33	0.17	0.11				0.25	0.15	0.09
	Long wet	0.30	0.17	0.11				0.22	0.14	0.09
2	Dry start	0.30	0.14	0.09	0.25	0.15	0.09	0.22	0.12	0.08
	Dry end	0.35	0.18	0.12	0.29	0.18	0.11	0.26	0.16	0.10
	Short wet	0.12	0.08	0.05	0.10	0.08	0.04	0.09	0.06	0.04
	Long wet	0.13	0.08	0.05	0.11	0.08	0.05	0.10	0.07	0.04
	Average	0.37	0.09	0.07	0.21	0.12	0.08	0.28	0.10	0.07

Figure 25 - Predicted densities (±SE) for individual surveys. Jackals were assumed to respond at all times over the same range as hyaenas.

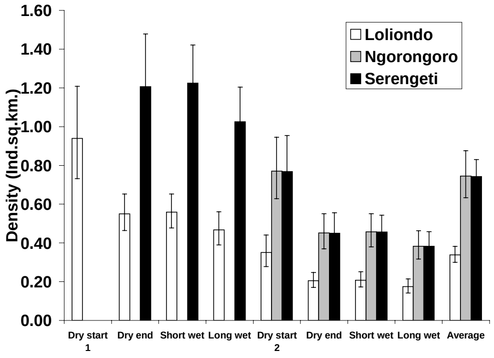
Black backed jackals



Golden jackals



Hyaenas



Lions

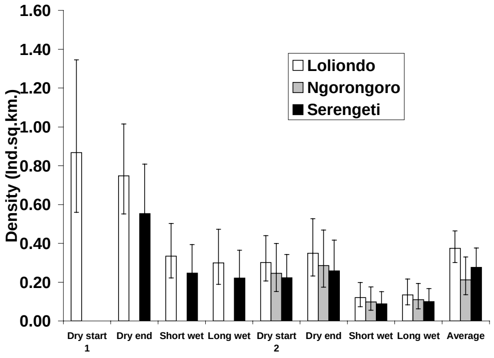
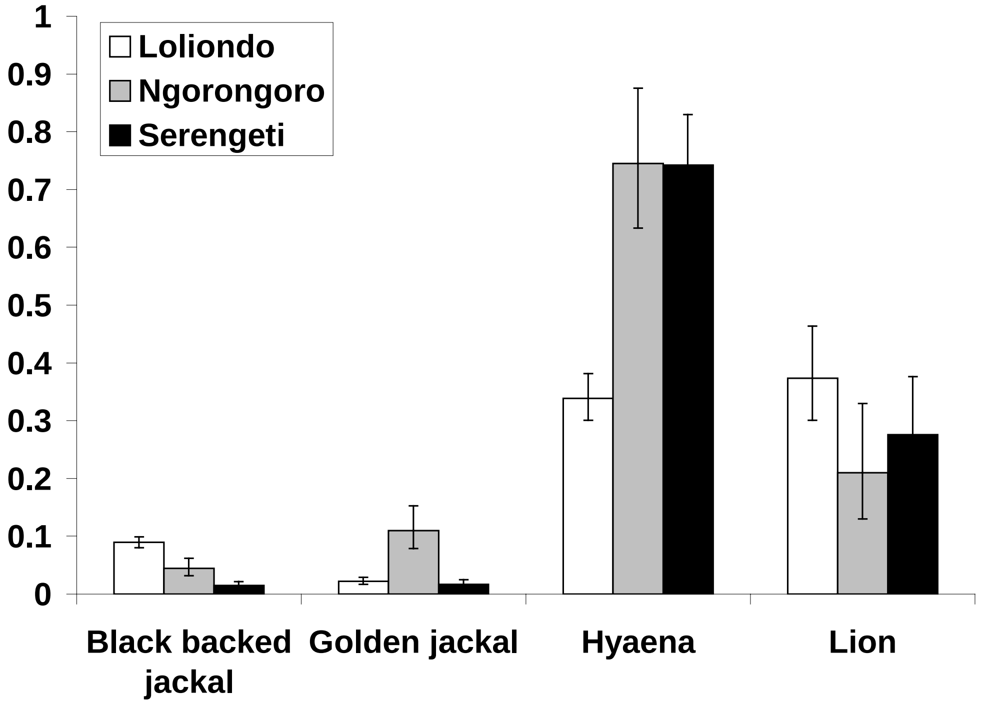


Figure 26 – Comparison of average density based on average IRREML estimates for all surveys and calibration results



Individual recognition of cheetahs

Total number of individuals seen

Photographs allowed the identification of a minimum of 88 independent (generally over 18 months) individuals present in the Serengeti study site, 24 in Loliondo and 19 in Ngorongoro. Most identified animals were female in the Serengeti and Loliondo but most in Ngorongoro were male. Adjusting the numbers of individuals seen for time showed that the Serengeti contained the highest number of individuals sighted per unit time whilst Loliondo and Ngorongoro showed similar total numbers but of these, more were independent in Ngorongoro (Table 26).

Table 26 – Number of individually recognised cheetahs identified in each study site

		Min. number of individuals[1]	Max. number of individuals sighted[2]	Sightings / year[3]
Serengeti	All ages	131	150	60
	Independent only	88 (55 female, 33 male)	104	41
Loliondo	All ages	63	76	32
	Independent only	24 (19 female, 3 male, 2 unknown)	32	12
Ngorongoro	All ages	33 (7 female, 11 male, 1 unknown)	36	33
	Independent only	19	22	19

[1] Number of clearly identified individuals

[2] Number of clearly identified individuals + all sightings that could not be identified

[3] Since only one year was spent in Ngorongoro and Serengeti sightings included a preliminary training period, number of individuals seen for one year is calculated.

Re-sighting rates

The total number of cheetah sightings in the Serengeti was 298, of which over half were re-sightings. However, re-sighting rates were much less frequent outside the park with only 28% of sightings in Loliondo seen before and 6% in Ngorongoro (Figure 27). However, the cumulative number of individuals recognised in each month increased steadily in all three sites with no evidence of any reduction in the number of new individuals seen later in the study (Figure 28).

Figure 27 – Total and % of total number of sightings that were either first time sightings or re-sightings

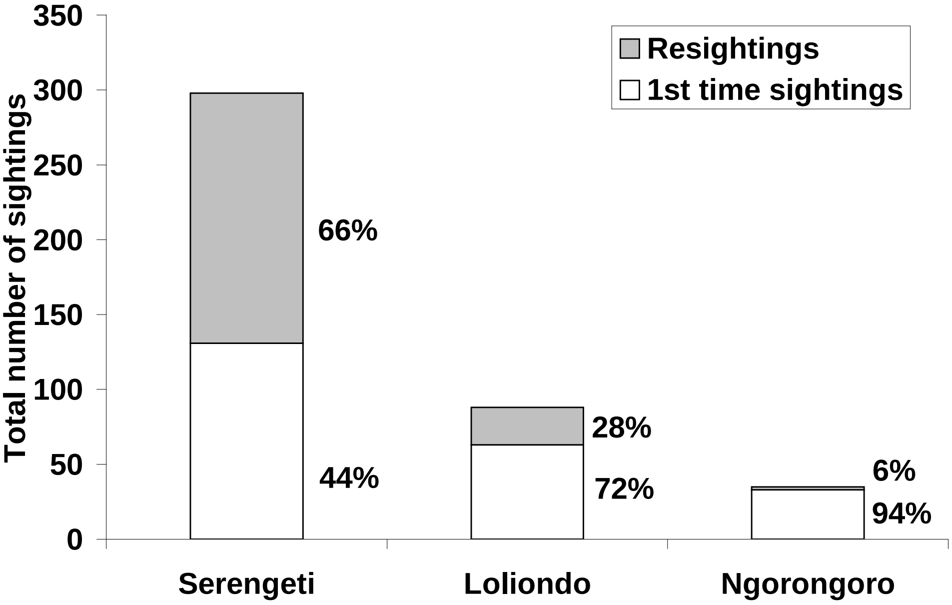
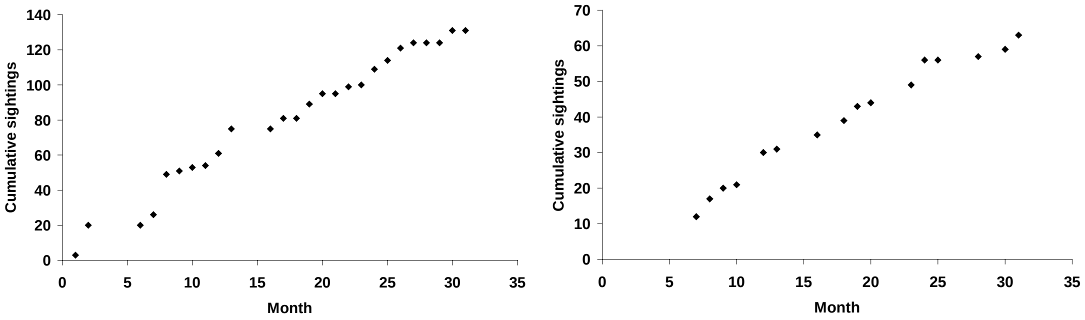
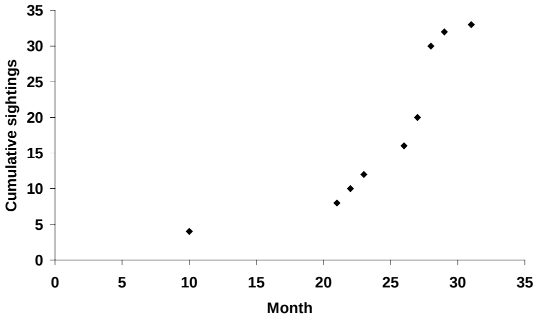


Figure 28 – Cumulative number of individually recognised cheetahs in A) Serengeti, B) Loliondo and C) Ngorongoro

A) **B)**



C)



4.5 Discussion

Diversity of species inside and outside the park

The responses to call-ins and sightings of cheetahs demonstrate that many large and medium-sized carnivore species occur outside the National Park with no major differences between the park and its buffer zones. The only exceptions were side-striped jackals, which only ever responded to call-ins inside the National Park, and striped hyaenas that were only seen in Loliondo. Responses by the striped hyaena were surprising, given that striped hyaenas tend to stop foraging before light, primarily feed on invertebrates in the Serengeti (Kruuk 1976) and actively avoid spotted hyaenas (Kingdon 1997). Although call-ins have been suggested as a survey tool for striped hyaenas (Mills 1998) and they are proficient scavengers (Kruuk 1976), there are no published results showing previous success at initiating a response. The absence of the striped hyaena from the open plains of the Serengeti and Ngorongoro was therefore unsurprising, despite their known presence in the park (Kruuk 1976). It is likely that responses were obtained in Loliondo due to the proximity to woodland cover (all responses were obtained in the far north of the study area, close to forest and rock cover) but it is also possible the lower levels of spotted hyaenas was influential. The responses of side-striped jackals were equally surprising. As with striped hyaenas, responses were not expected since side-striped jackals generally occupy more wooded and human-disturbed habitats (Kingdon 1977) and they are thought to feed primarily on small mammals and fruit (Atkinson *et al.* 2002). However, conclusions are hard to draw on the differences due to the infrequency of responses.

Carnivore abundance outside the national park

Large carnivore abundance estimated by call-ins was not significantly higher inside the park than in the buffer zones where humans were present. In contrast, more of the major jackal species were seen outside the park, with black backed jackals more common in Loliondo and golden jackals more common in Ngorongoro. Hyaenas were equally likely to appear at all-ins in all regions, although significantly more individuals were seen in the Serengeti, and neither the proportion of responses or numbers of individuals of lions differed between each of the regions. Preliminary estimates of cheetah numbers suggested that numbers were lower outside the park, however re-sighting rates indicated that a relatively small proportion of the population was sighted in each area, particularly outside the park. Such findings are highly surprising and important. Although it was expected that carnivores would be present in the buffer zones, it was assumed that the presence of humans would cause some reduction in densities, as found in almost every other study of carnivores in relation to humans, including previous surveys in Loliondo *e.g.* (Borner 1992), (Caro 1999d), (Woodroffe 2000). Some of the variation may be due to variation in habitat that could not be controlled for in the experiment. For example, black backed jackal densities were possibly influenced by preferences for savannah habitats bordering woodland as was more common in Loliondo rather than completely open grassland habitats, which tend to be dominated by golden jackals (Lamprecht, 1978, quoted in (Estes 1991)). Differences between golden jackals in the Serengeti and Ngorongoro might be due to differences in rainfall, with golden jackals best adapted to drier conditions (Estes 1991) as found closer to the rain shadow of Ngorongoro crater (Sinclair 1979). Although it is surprising that the protected National Park plains appear to hold significantly fewer jackals than the plains in the buffer zones, jackals are known to tolerate human presence in some areas (Kingdon 1997). Hyaenas were the only carnivore that existed at higher densities inside the park. This could be a reflection of adult mortality outside the park *e.g.* (Hofer & East 1995), (Hofer *et al*. 1996) although this is thought to be primarily due to snaring which would be expected to affect all carnivores equally. Alternatively, it may be a reflection of the limitations of the study (p.154). The results for lions may also be influenced by habitat to some degree, since the open plains of the Serengeti are not necessarily the optimal habitat for lions (Schaller 1972b) and higher densities would be expected nearer the woodland edges where as the Loliondo study area included vegetated drainage lines which may have provided cover. Lions are known to be able to survive in semi-protected areas to some degree (*e.g.* (Creel & Creel 1997), (Frank 1998) but most studies show lion densities to be heavily affected by human presence *e.g.* (Borner 1992), (Hunter 1996), (Bauer *et al*. 2001). Although these findings do not necessarily show that the whole of the buffer zones support equivalent populations of carnivores to the national park, since only a restricted area and habitat type was surveyed, they do show that under certain conditions semi-protected areas have the capacity to hold substantial populations of large carnivores and that human presence does not necessarily lead to carnivore demise (Linnell *et al*. 2001). Such findings cause great optimism for large carnivore conservation since, when dealing with relatively small population sizes, the existence of even a small number of additional individuals beyond protected areas could substantially raise the viability of a population *e.g.* (Kenney *et al*. 1995), (Gaona *et al*. 1998), (Kelly & Durant 2000).

Seasonal variation

Seasonal variation was significant for most analyses of responses, although obscured to some degree by the decreasing responses over time likely due to habituation. For all species, a significantly higher chance of response was exhibited in the start of the dry season, constant between regions and years. However, seasonal fluctuation in the actual number of responses was more variable. Seasonal variation in responses in carnivores could be due to two factors. Firstly, responses may vary with movement in and out of an area as the carnivores track prey availability. Secondly, the chance of a response may vary with season. In the first case, responses would be expected to be positively correlated with local prey density. In the second case, responses would be expected to be negatively correlated with prey density.

Although responses of black backed jackals were more likely in the short dry season, seasonal variation was insignificant for the number of responses, perhaps because larger groups (with cubs) responded in the wet seasons. However, the number of golden jackal responses did fluctuate with season, although differently in each region and each year, although responses were highest in the two dry season surveys on all occasions. Seasonal movement of jackals would not be expected to cause variation in the number of responses since both black backed and golden jackals are known to occupy permanent territories throughout their lives on the Serengeti plains, surviving on invertebrates during the dry seasons (Moehlman, 1983, quoted in (Estes 1991)). Although territory sizes vary with resource availability, thus allowing a given area to hold more or less pairs, it is unlikely major changes would occur over the course of a year. Therefore, the increased responses in the dry seasons are likely to be due to a change in the chance of response, with well-fed animals less likely to scavenge in the wet season. However, this is not supported by local prey densities with neither species showing reduced responses when prey densities were higher. This could be a reflection of local prey density not being a good indication of jackal food availability or it could be an indication that jackal variability was not driven by variation in the chance of response or the local jackal population size but either stochastic or otherwise unmeasured effects.

Hyaena responses also varied seasonally and constantly between years, but differently between regions, with more responses at the start of the dry in Loliondo and Ngorongoro but later, in the end of the dry and start of the wet season, in the Serengeti. Hyaenas are known to move extensively in order to track prey availability (Hofer & East 1993c), with up to 100% of clan members commuting outside the clan territory to other territories during the dry season when resources were low (Hofer & East 1995). In this study, the effect of prey on hyaena responses was significantly positive for both chance of a response and the total number responding, suggesting that some of the seasonal variation was due to seasonal movements in response to prey availability. However, Ogutu and Dublin (1988) showed that a decreasing response occurred for hyaenas with increasing prey. It is therefore likely that both effects were operating on hyaena responses at the same time and periods of increased responses during high prey densities were in fact probably underestimates.

The number of lion responses also varied significantly with season, but constantly across years and region, with the highest number of responses during the two dry season surveys. Lions also move to some extent with prey availability, with nomadic lions following the migratory prey relatively closely and resident prides, limited by a relatively immobile period when cubs are young, shifting their movements towards areas of higher prey concentration when local availability falls (Schaller 1972b). However, as with jackals, local prey availability appeared to have no effect on lion responses suggesting that higher responses were not due to more lions in the area due to increased prey availability. Since prey did not have a negative effect, it is either possible that variation was due to a random or unmeasured factor, or that measures of prey availability did not accurately reflect true availability to lions.

Due to the contrasting effects in operation during high prey availability, call-ins are probably not a particularly reliable indicator of seasonal fluctuation without detailed calibrations showing the effect of local prey levels on response proportions. Similar conclusions were drawn by Ogutu and Dublin (1998) who recommended surveys should only be carried out at periods of low prey density.

Implications for cheetah success outside protected areas

The results of the call-in survey combined with the data collected on number of individual cheetahs seen do not support the theory that cheetah numbers would be higher relative to lions and hyaenas outside the park. In contrast, lions in particular occur at equivalent densities outside the park, whilst fewer cheetah individuals were seen outside the park. In terms of abundance this suggests that the relative density of cheetahs is *reduced* relative to larger carnivores outside the park and that the advantages expected due to reduced densities of lions and hyaenas outside the park (Laurenson 1995b) are unlikely to occur. However, this does not necessarily disprove the hypothesis that cheetahs will be more *successful* outside the park. This is because firstly densities are not necessarily reflective of success; for example density is not a reliable predictor of source-sink relationships and source populations can be smaller than the sink populations that they feed (Watkinson & Sutherland 1995), (Dias 1996). Secondly, the influence of the large carnivores on cheetahs may not be simply controlled by relative densities. Although increased densities of cheetah predators may increase predation risk, many other factors outside the park, such as activity times, may counter this effect (see Chapter 6).

Comparisons with previous work

Comparisons were then made with previous surveys of carnivores in the Serengeti and elsewhere in Tanzania. In general, previous Serengeti surveys from the long grass plains represent the Serengeti study site from this study and the short grass plains are contiguous with the Ngorongoro plains from this study. Results from this study were presented as the overall estimate for the two year study and the range of individual survey estimates. The results for jackals show density estimates similar to those calculated by transects in 1977 and 1986 inside the National Park. Black backed jackals in the Serengeti study area were very similar to estimates from the long grass plains whilst Ngorongoro estimates were close to the 1986 short grass plains, not the higher 1977 estimates. Overall Loliondo estimates were very similar to estimates for the Serengeti as a whole, which included habitats other than open grassland. Golden jackal estimates for the Serengeti were also comparable to previous estimates of the long grass plains. However, despite being significantly higher than the Serengeti estimates, even the highest estimates from Ngorongoro were much lower than found on the short grass plains in the past. They were also at surprisingly low densities in

Loliondo. Golden jackals are listed as not endangered (IUCN 2002a), indeed are often the most numerous carnivore on east African grasslands (Estes 1991), suggesting that numbers had possibly fallen in the areas surveyed (

Table 27).

The range of hyaena densities for the Serengeti was similar to previous estimates for the long grass plains, although the overall estimate was much higher. Estimates for Ngorongoro were lower than the short grass plain estimates for the Serengeti whilst the Loliondo estimates were lower than any previous estimates from the Serengeti although still higher than several other protected areas in Tanzania (although at their peak, Loliondo densities were comparable to previous Serengeti estimates). However, calculation of spotted hyaena densities in the Serengeti ecosystem are confused by the existence of the commuting system whereby hyaenas travel long distances from the den in order to exploit migratory prey (Hofer & East 1993c). Since commuters are tolerated by local residents, a survey will probably include a certain proportion of resident and commuting hyaenas at any one time (Hofer & East 1995). Thus, in the dry season a survey may reveal a small proportion of the local population whilst in the wet season it will include many individuals commuting from outside. Hofer and East (1995) devised a method to counteract this, using a formula based upon a dry season (June to December) estimate, a wet season (January to May) estimate and estimated proportions of individuals from a clan commuting during the wet and dry seasons based upon known individuals (Hofer & East 1995). However, such calculations could not be carried out on call-in estimates due to the likely unequal response proportion in different seasons as described above making an accurate estimate in the dry *and* wet season impossible. Therefore, although density calculations are probably useful estimates of the number of hyaenas in an area at any one time, they do not allow calculation of the probably resident population (Table 28).

Estimates of lion densities from the call-in study for the Serengeti and Ngorongoro sites compared with the upper estimates from previous studies; overall densities of around 0.3/km^2 in the Serengeti site were similar to the 1977 survey of the long grass plains whilst the peak of over 0.5 lions / km^2 was far higher and about five times higher than the 1986 estimates. Estimates from Ngorongoro were also similar to the upper 1977 estimates of Serengeti short grass plains densities whilst Loliondo estimates were comparable to the highest previous records for the Serengeti and, at their peak, exceeded density estimates from Manyara National Park, one of the highest density estimates on record. The results were even high compared to the range

of densities recorded across sub-Saharan Africa which range from 0 up to over 0.3 individuals per km^2 (IUCN 2002b). It is feasible that numbers were particularly high in the study areas chosen since local lion densities can vary enormously depending on prey distribution (Schaller 1972b) and lion populations have been recovering since an epidemic of canine distemper in the 1980s (Roelke Parker *et al*. 1996), (Packer *et al*. 1999). Caution should be taken extrapolating the results, since variability in lion distribution means that surveying relatively limited sample areas can lead to meaningless results for larger areas (Schaller 1972b), and various other factors limit the accuracy of call-ins (see “Limitations of the study”, p.154). However, the call-in results do suggest that lion populations were equally healthy in the study areas inside and outside the park and persisting at densities comparable to the healthiest populations in recent history (
Table 29).

Table 27 – Estimates of jackal densities in areas of Tanzania (in order of golden jackal density).

Region	Details	Golden jackals (Ind. / km^2)	Black backed jackals (Ind. / km^2)	Source
Serengeti long grass plains	1977 wet	0	0.02	SRI (1977), quoted in (Hofer & East 1995)
Serengeti long grass plains	1986 wet	0.02	0	(Campbell & Borner 1986)
Serengeti long grass plains	1977 dry	0.02	0.2	SRI (1977), quoted in (Hofer & East 1995)
Serengeti plains	**1999-2001**	**0.02 (0-0.04)**	**0.02 (0.01-0.03)**	**This study**
Loliondo plains	**1999-2001**	**0.02 (0-0.15)**	**0.1 (0.04-0.22)**	**This study**
Ngorongoro plains	**1999-2001**	**0.12 (0.01-0.11)**	**0.05 (0.02-0.03)**	**This study**
Serengeti total	1977 dry	0.42	0.07	SRI (1977), quoted in (Hofer & East 1995)
Serengeti short grass plains	1977 dry	0.54	0.03	SRI (1977), quoted in (Hofer & East 1995)
Serengeti total	1986 wet	0.54	0.02	(Campbell & Borner 1986)
Serengeti total	1977 wet	0.61	0.16	SRI (1977), quoted in (Hofer & East 1995)
Serengeti short grass plains	1986 wet	0.67	0.02	(Campbell & Borner 1986)
Serengeti short grass plains	1977 wet	0.79	0.2	SRI (1977), quoted in (Hofer & East 1995)

Table 28 – Estimates of spotted hyaena densities in areas of Tanzania (in order of density).

Region	Details	Hyaenas (Ind / km^2)	Source
Katavi NP		0.18	(Caro 1999a)
Serengeti short grass plains	1977 dry	0.22±0.08	(Hofer & East 1995)
Serengeti plains total	1977 dry	0.28±0.06	(Hofer & East 1995)
Selous GR	1994	0.32	(Creel 1996)
Loliondo plains	**1999-2001**	**0.34 (0.17-0.94)**	**This study**
Serengeti long grass plains	1977 wet	0.42±0.14	(Hofer & East 1995)
Serengeti long grass plains	1986 wet	0.42±0.27	(Campbell & Borner 1986)
Serengeti long grass plains	1977 dry	0.43±0.18	(Hofer & East 1995)

Region	Details	Hyaenas (Ind / km^2)	Source
Serengeti source population	1986	0.6	(Hofer & East 1995)
Ngorongoro plains	**1999-2001**	**0.74 (0.38-0.77)**	**This study**
Serengeti plains	**1999-2001**	**0.74 (0.38-1.22)**	**This study**
Central Serengeti	1987-92	0.8	(Hofer & East 1993a)
Serengeti plains total	1977 wet	1.12±0.15	(Hofer & East 1995)
Serengeti short grass plains	1977 wet	1.29±0.19	(Hofer & East 1995)
Serengeti plains total	1986 wet	1.52±0.24	(Campbell & Borner 1986)
Ngorongoro crater	1966-8	1.7	(Kruuk 1972)
Serengeti short grass plains	1986 wet	1.80±0.30	(Campbell & Borner 1986)

Table 29 – Estimates of lion densities in areas of Tanzania (in order of density).

Region	Details	Lions (Ind / km^2)	Source
Katavi Game Controlled Area		0	(Caro 1999d)
Masai Steppe		0.003	(Lamprey 1964)
Serengeti short grass plains	1977 dry	0.01	SRI (1977), quoted in (Hofer & East 1995)
Total Serengeti plains	1977 dry	0.03	SRI (1977), quoted in (Hofer & East 1995)
Katavi NP		0.07	(Caro 1999a)
Serengeti short grass plains	1986 wet	0.08	(Campbell & Borner 1986)
Total Serengeti plains	1986 wet	0.08	(Campbell & Borner 1986)
Serengeti (whole)		0.08-0.09	(Schaller 1972b)
Serengeti long grass plains	1986 wet	0.1	(Campbell & Borner 1986)
Serengeti long grass plains	1977 dry	0.12	SRI (1977), quoted in (Hofer & East 1995)
Serengeti short grass plains	1977 wet	0.17	SRI (1977), quoted in (Hofer & East 1995)
Ngorongoro plains	**1999-2001**	**0.21 (0.10-0.29)**	**This study**
Total Serengeti plains	1977 wet	0.22	(Hofer & East 1995)
Ngorongoro Crater		0.27	(Schaller 1972b)
Serengeti plains	**1999-2001**	**0.28 (0.09-0.55)**	**This study**
Serengeti long grass plains	1977 wet	0.38	SRI (1977), quoted in (Hofer & East 1995)
Loliondo plains	**1999-2001**	**0.37 (0.12-0.87)**	**This study**

Region	Details	Lions (Ind / km^2)	Source
Manyara NP		0.38	(Schaller 1972b)

Limitations of the study

Several factors may have biased the number of responses and / or the density estimates based on them. Of primary importance was the effect of year, which explained a significant proportion of variation in all tests. In every case, responses in year 2 were significantly lower. In the cases where the effect of year varied by region this was because the reduction in year 2 was greater in one region than another. These reductions in responses may reflect one of two things. Firstly, actual declines in numbers may have occurred in year two resulting in fewer responses. Secondly, habituation to call-ins may have reduced the chance of responses. Annual variation in numbers is possible, especially for hyaenas due to their high mobility (Hofer & East 1993a) and possibly lions (Scheel & Packer 1995). However, habituation is also a major concern. Call-ins in this study were played in a given location for one hour four times a year. It has since been recommended that call-ins should not be repeated more than twice a year or to vary the sounds used to attract animals to avoid habituation (Mills *et al*. 2001) or to offer rewards (Smuts 1977), (Mills *et al*. 2001). Furthermore, it may not be necessary to play the tape for one hour continuously. Ogutu and Dublin (1988) played the calls for fifteen minutes with three minute intervals every five minutes whilst Mills (2001) played calls for a maximum of eighteen minutes with five minute intervals every six minutes. Playing the tape for one hour may have maximised responses on initial surveys, since lions especially were found to arrive over 50 minutes from the start, but it was likely to have increased the effect of habituation on subsequent surveys. Furthermore, is not known whether playing the tape for the full period initiated more responses than playing the tape for a shorter period and sitting silently for the remaining time. The effects of year were probably a combination of changes in carnivore densities and habituation. However, the increases in prey density in the second year (see chapter 3) and the steady decline of responses between seasons within years (see individual graphs of responses over time) suggest that habituation was the key factor. If so, the effect of year may be underestimated due to the absence of data for Ngorongoro for the first year thus introducing data unaffected by habituation in the second year. The effects of habituation may therefore indicate that the first year of data for each region are more likely predictors of true population sizes than the combined dataset.

Secondly, the assumption of response proportions may have been inaccurate for both relative abundance and actual density estimates. When comparing relative densities, response proportions were assumed to be equivalent in all areas. There are various scenarios where this might be an incorrect assumption. For example, it might be hypothesised that carnivores outside the park were hungrier and more likely to respond than inside the park, or shyer and less likely to respond. Alternatively, responses may have varied with small differences in habitat between the three regions. This could be behavioural. For example, scavenging by lions in woodland habitats has been shown to be less important than on the Serengeti plains (22% of kills *vs.* 50%) (Schaller 1972b) which could indicate a decreased likelihood of response to the tape in wooded areas or environmental, due to the increased audibility and visibility in more open, flat areas. Unfortunately, since lions and hyaenas were almost never seen outside the park except during call-ins, calibrations outside the park were impossible and thus this effect was untested. However, habitat differences were controlled for as far as possible by selecting only open areas in each region. Any small differences in topography or vegetation would be unlikely to have significantly affected audibility or visibility (for example of vultures landing).

Estimates of response proportion would also have influenced density estimates. Although the results for lions were similar to those found by Ogutu and Dublin (1998), the results for hyaenas were much higher than found by Mills (2001), despite Mills’ prediction that whilst response range will vary with location, behavioural differences should be minimal (Mills *et al.* 2001). This could be due to Serengeti hyaenas being more responsive, or it may be an artefact of the relatively small proportion of calibrations carried out within the audible range Estimates of response proportions for jackals were especially vulnerable to error since no calibration data were available. Various factors exist that may have reduced the chance of response. For example, jackals are territorial, which may affect response to call-ins; golden jackal territories are 2-4 km^2 , black backed jackals are 2.5 km^2 and both permanent for life, although the size can vary depending on resources. Thus an area can hold more pairs after several good years (Moehlman, 1983, quoted in (Estes 1991)). Since the audible range was assumed to cover an area far larger than a single territory, it might be possible that crossing territory borders was as inhibition to responses for some jackals. However, there is evidence that territoriality may not have had a major influence with up to six pairs of black backed jackals being recorded to converge on a large carcass (Moehlman, 1983, quoted in (Estes 1991)). This was supported by observations at call-ins, with multiple pairs frequently arriving from different directions and occasional chases between pairs (*pers. obs.*). Alternatively, it might also be argued that the fact that scavenging forms a minor part of jackal diet. An estimated 6% in the Serengeti (P.D. Moehlman in (Macdonald 1995)) compared to approximately 30% for spotted hyaenas in the Serengeti (Kruuk 1972) and over 50% for lions (Schaller 1972b) – might lead to a lower response proportion than used in calculations here. However, the lower importance of scavenging in hyaena diet compared to lions was not reflected in the proportion of responses, therefore the percentage occurrence in diet is probably a reflection of availability of scavenging opportunities rather than preference.

Finally, calculations of cheetah numbers were subject to a variety of limitations. Using individual sightings to estimate the size of an open population is subject to a range of limitations (*e.g.* see (Cooper & Durant, in press)). Of particular concern in this study was the re-sightings rates which suggested that despite two years of intensive survey effort, either only a small fraction of the populations were seen or population composition was highly dynamic. This is because although new sightings would be expected throughout the study as recruitment occurs it would be expected that the rate of new sightings would decrease as more of the population was surveyed (Sutherland 1996). In contrast to this, the rate of sightings appeared to be the same at the end of the project as at the beginning. It is possible that this reflected a population consisting of a high proportion of dispersing animals (*e.g.* see (Thomson *et al*. 1992), (Caro 1994), (Beier 1995)), which might even represent a sink population (Lariviere *et al*. 2000), with the high proportion of males in Ngorongoro lending some weight to this idea. However, Loliondo and to some extent Ngorongoro data also described a large number of breeding females and a resident population of some size definitely existed. The likelihood is that sampling effort would have to be increased to get sufficient data for mark-recapture analysis to get more confident estimates of abundance.

However, despite the limitations, it is thought that the call-in methods used in this study still provided a highly effective comparison of carnivore densities. Improvements could have been made with further calibrations, but the incorporation of wind factors into the likely response range represent an improvement on previous surveys.

Chapter 5: An evaluation of methods used to survey carnivores in semi-protected areas

5.1 Summary

In the literature describing methods for surveying carnivores there is a wide range of techniques. For the carnivore survey described in chapter 4, two different methods were used to survey carnivores. However, during the study several other techniques were also used. Since this study required the comparison of carnivore surveys carried out in two different areas (one without people present and one with people present) there was concern that different census techniques may suffer different biases in each area. This chapter therefore compares the “true” results from chapter 4 with some of the other most common techniques used in the literature for to test whether differences in study site can affect validity of the survey method used. Alternative methods include estimates of relative abundance based on 179 questionnaires, an observation-based index covering 35,000 km, 8 line transect surveys and the results of density predictions based on prey biomass availability. The results show that all techniques agree generally on relative abundance, placing spotted hyaenas as the most abundant and lions as the second most abundant. However, sightings-based methods predicted far lower densities outside the park and prey biomass estimates overestimated cheetah abundance. Actual density estimates were more varied. Jackal estimates, based on transects and call-ins agreed on approximately 0.05-0.15 jackals per km^2. Hyaena estimates outside the park were particularly low compared to call-in estimates of around 0.5-1 / km^2. However, if migrant species or livestock were included, biomass estimates predicted far higher hyaena estimates. Lion estimates were similar, underestimated by all methods compared to call-ins but overestimated when biomass included livestock and migrants. The results showed a particularly strong limitation of visual-based techniques outside the park, with estimates based on road sightings or transects working relatively well inside the park but poorly outside in comparison to call-ins. For lions, these methods predicted zero densities in Loliondo. This has serious implications for previous surveys of carnivores outside parks, which generally rely on sightings-based methods. Biomass- based methods were also shown to be of limited use depending on which prey were included. Biomass methods were particularly inaccurate for cheetahs.

5.2 Introduction

The range of carnivore monitoring techniques

Monitoring of carnivore abundance is fundamental to carnivore research, conservation and management (Wilson & Delahay 2001). However, the apparently simple task of describing the size and extent of population of carnivores within a given area can be extremely difficult to achieve due to their low densities, cryptic and nocturnal behaviour, large home ranges, occupation of a range of habitats and varying social systems (Gese 2001), (Wilson & Delahay 2001). A wide range of methods exists for surveying carnivore populations, allowing estimates to be made at a variety of levels of complexity. Firstly, predictions can be made for carnivore presence and even abundance based on known environmental variables and previous studies of species preferences. Secondly, data can be collected to show definite presence or absence and distribution of a given species. Thirdly, information on relative abundance can be obtained using indices. Fourthly, actual abundance can be estimated using sampling or, ideally, total counts completed.

Indices of relative abundance

Indices can be used to describe a portion of a population, giving information on presence or absence and limited information on abundance. Although the precise nature of the relationship between the index result and the actual population abundance might not be known, if it is constant it can allow comparisons of relative density between different areas (Sutherland 1996). Generally indices are based on signs of carnivore presence. These include interviews with local wildlife workers, residents or tourists and have been used to survey wild dogs (Ginsberg *et al*. 1997), foxes (Heydon *et al*. 2000), cheetahs (Gros *et al*., 1996, , lions (Bauer *et al*. 2001) and hyaenas (Mills 1998). Alternatively, tracks and spoor can be used to compare relative abundance (*e.g.* (Mahon *et al*. 1998), (Stander 1998), (Scott 2000)), or counts of calls have been used (Hofer and East, unpublished, quoted in (Sutherland 1996)). Indices can also be based on actual observations by recording the number of sightings whilst controlling for search effort (Gese 2001) and these have been used successfully for various species *e.g.* cats, dingoes and foxes (Mahon *et al*. 1998). Although abundance indices have the advantage of being relatively easy to carry out, and are sometimes the only viable way of obtaining information on some carnivore populations, they do depend upon the relationship between the relative estimate and the actual density being constant. Often this might not be the case due to variation in season, habitat, or other factors. Few indices have been compared with known density values and therefore often their reliability is not fully known (Gese 2001) although see (Stander 1998).

Estimating density

Transects

Estimates that are more useful can be made by calibrating indices based on signs or by taking into account the area searched when counting observations, thereby allowing actual density estimates to be calculated. The most common method is the use of transects. Ideally transects would cover the entire study area to give a total count. Total counts are frequently used for large, conspicuous mammals such as large herbivores (*e.g.* (Watson 1969), (Campbell & Borner 1995)) but less frequently for the more cryptic carnivores that require more intensive searching in restricted areas, although an exception is provided by a helicopter survey of lions in a Serengeti buffer zone (Borner 1992). More commonly, transects sample a limited proportion of the study area and extrapolate to calculate overall densities. Transects include strip transects, which carry out a total count in a number of transects with a predefined width, such as used on ground-based surveys for a variety of carnivores (Anon. 1977 quoted in (Hofer & East 1995)). They also include counts of several species (*e.g.* (Caro 1999a), (Caro 1999d)), use of spotlighting for night surveys (Sharp *et al*. 2001), (Scott *et al*., in submission) or from aircraft (*e.g.* (Campbell & Borner 1986), (Borner 1992)). A refinement of the strip transect census are line transect surveys analysed using the distance sampling method (Buckland *et al*. 1993) which do not predefine the area censused but use the distance from the line of each sighting to estimate unrecorded sightings on the survey. This technique has been used for foxes (Heydon *et al*. 2000), however, although able to produce more accurate estimates of abundance (Cassey & McArdle 1999), (le Mar *et al*. 2001), distance sampling requires large numbers of sightings for accurate analysis (Buckland *et al*. 1993) thus limiting its use with low density carnivore populations.

Attracting carnivores

An alternative range of methods relies upon attracting responses from carnivores. Using a lure such as a scent, a sound recording and/or sometimes bait to either attract or stimulate a response from carnivores, the study area is censused in a series of point transects, recording the number of animals responding to, or approaching, the station to give an index of population size. If the responses are also calibrated, estimating the detectable range of each playback or scent station and the proportion responding, calculation of actual densities is also possible. Although response to recordings is generally limited to adults only, and both techniques are limited by the availability of suitable audio or scent cues, call-ins using recordings of feeding hyaenas have been used successfully attract and survey lions (Ogutu & Dublin 1998) and spotted hyaenas, (Mills *et al*. 2001). Scent stations have been used for a range of species (Sargeant *et al*. 1998) and replies to lion roars have been used to survey lions, although relatively unsuccessfully (Schaller 1972b).

Capture-mark-recapture

Other methods rely on capture-mark recapture methods, based on an initial survey round, marking individuals and subsequent survey rounds recording the number of marked individuals re-censused (Sutherland 1996). “Captures” can be physical captures using traps or darting with anaesthetic (*e.g.* (Corn & Conroy 1998), (Kruuk 1972)) with marking also a physical process such as use of ear tags (*e.g.* (Kruuk 1972), (Schaller 1972b) or “captures” can be sightings using natural markings for identification, removing the need for handling. Individual recognition based on natural markings has been successfully demonstrated for a range of carnivores. Cheetahs (Caro 1994), spotted hyaenas (Hofer & East 1993a), tigers (Karanth 1995) and wild dogs (Maddock & Mills 1994) have all been identified based on coat patterns. Lions have been identified based on facial markings (Pennycuick 1970) and mountain lions based on footprints (Grigione *et al*. 1999). High reliability of distinguishing individuals has been shown in several of these examples *e.g.* (Pennycuick 1970), (Caro & Durant 1991). If sufficient sightings are obtained, individually known animals may be used to obtain a total count within a given area such as achieved with long-term studies of cheetahs on the Serengeti plains (Caro 1994) and lions in parts of the Serengeti and Ngorongoro crater (*e.g.* (Hanby *et al*. 1995)). Alternatively, mark-recapture analysis can be used with a range of methods available including the Lincoln index (whereby a closed population is assumed) as used for hyaenas (Kruuk 1972) or more complex methods taking into account immigration, emigration and unequal sighting probabilities as used for cheetahs (Cooper & Durant In press). A variation on methods using individual recognition is the analysis of tourist photos as demonstrated for wild dogs (Maddock & Mills 1994) or cheetahs (Bowland 1995), (S.Durant, *pers. com*) or the use of camera traps that are triggered by passing animals *e.g.* (Karanth & Nichols 1998), (Carbone *et al*. 2001).

Estimates of density based on environmental predictors

Because of the various difficulties and effort required for surveying carnivores there is a strong interest in methods that can accurately predict population densities based upon more easily measured variables (see Gros *et al*., 1996 for a review). Estimates of carnivore distribution based on environmental parameters are quick and easy, allowing rapid estimates with little or no fieldwork. Identification of the important variables required for prediction has been tricky, with densities for several species varying by a factor of 100 depending on the conditions of the study (Carbone & Gittleman 2002). However, parameters that have been used include prey availability, based on regression of carnivore biomass against prey biomass, (Carbone & Gittleman 2002), (Gros *et al*. 1996), habitat availability (Gros & Rejmanek 1999) and estimates based on area availability and average range sizes (Gros *et al*. 1996), (Mills 1998). At minimum, use of environmental parameters can predict likely presence and absence of a species. However, with careful calibration environmental parameters may also be used to estimate likely densities of certain species, a technique that has been applied to estimates based on prey availability (Carbone & Gittleman 2002). Concurrent to the interest in abundance estimates have been various theoretical ecology studies on biological scaling, relating population densities to body size and resource use or availability (see Carbone & Gittleman (2002) for a review). In both fields the relationship between prey population size and carnivore density has held great interest. The accuracy of using prey to estimate carnivore density has been questioned since it relies heavily on accurate identification and weighting of the influential variables, and for cheetahs the results have been shown to underestimate true densities (Gros *et al*. 1996). However, Carbone *et al* (2002) have shown that a very strong, linear relationship exists between carnivore densities and average prey biomass, regardless of other factors (Carbone & Gittleman 2002).

Chapter aims

The aim of this chapter is to examine whether the choice of survey method is important when measuring large carnivore abundance in semi-protected environments. In order to achieve this, three questions were examined:

1. What do the various methods predict for relative abundance of each carnivore inside and outside the park? Do they each agree?
2. What does each method predict for actual densities inside and outside the park? Do all methods agree?
3. What do the results suggest for future and previous carnivore surveying?

5.3 Methods

Choice of methods

The chosen methods for chapter 4 were the use of call-ins, attracting scavengers to recordings of hyaenas on a kill, to census lions, spotted hyaenas and jackals and individual recognition to survey cheetahs. Call-ins were chosen due to proven success and accuracy in similar habitats (Ogutu & Dublin 1998) whilst individual recognition has been established as the best method for surveying cheetahs in the Serengeti (Caro 1994) and both methods produced estimates of carnivore abundance inside and outside the park (Chapter 4). The choice of comparative methods was limited partly by the conditions of the study (for example, camera trapping is unsuitable for open habitats with few pre-defined carnivore pathways; resources were not available for aerial surveys and the areas were too large to consider scent stations or indices based on spoor). However, the chosen methods cover the most commonly used in the literature, including indices of relative abundance based on interviews and on direct observations, estimates of density based on transects and a prediction of density based on environmental parameters.

Call-ins and individual recognition

Methods and results for the call-in survey and individual recognition-based estimates are presented in chapter 4. The estimates of density from call-in surveys conducted at three monthly intervals, starting in July 99 and ending in April 2001, together with overall estimates of cheetah abundance in each region are used for comparison for this study.

Questionnaire-based index of relative abundance

A survey of relative abundance based on questionnaires was incorporated into a social survey investigating Maasai relationships with carnivores in the two study sites outside the Serengeti (Chapter 7). The questionnaire was semi-structured and directed at adult men and *murran* (teenage “warriors”) living in the vicinity of the carnivore surveys. Initial questions were asked to determine attitudes and knowledge of the individual species, after which photographs were used to ensure that both the respondent and interviewer were discussing the same species. Questions were then asked on the last time each species had been sighted personally by the respondent. The survey was intended to quantify contact rates between Maasai and each of the carnivore species, but assuming equal sightability for each species, the relative timing of the most recent sightings was also taken to be a measure of relative abundance. For full details on methods, see chapter 7.

Observations-based index of relative abundance

A predator population index was created by recording the time spent and distance travelled for each car trip undertaken in each region and noting all large predators seen during the trip. Trips were not undertaken specifically to compile the index; rather the data were collected opportunistically during almost any journey made during the study. Thus, a trip could include a journey between two points, or it could include a journey to survey prey density or search for cheetahs. Nevertheless, search rate was controlled for in the analysis. Only time spent travelling was included in the trip time and every trip was located entirely within the borders of one of the study areas. If a border between study areas was crossed, a new trip record was started. Only predators initially sighted by the author were included in the analysis. The few sightings made with the aid of tourists or other researchers were excluded since few such aids were available outside the park.

Analysis was carried out individually for cheetah, lion and hyaena sightings only. Data were initially examined using mean sightings per kilometre to demonstrate the actual sighting frequencies during fieldwork. To account for variation between individual trip conditions other than effect of the study area, further analysis was then carried out using a Generalised Linear Model (GLM), defining Poisson errors and a log link function as appropriate for count data (Crawley 1993). Analysis was carried out at two levels for each species; numbers of *independent sightings or groups* seen per 100 km driven were analysed, to show sightings frequency and numbers of *actual individuals* per 100 km, correcting for over-dispersion to account for non-independence of individual animals, were analysed to give an index of actual population size. The effects of four potential explanatory variables were incorporated as model terms (Table 30).

Table 30 – Explanatory variables used as model terms for explaining the variation in numbers of predators seen on logged trips.

Model term	Description
Region	Region describes the study areas Loliondo, Ngorongoro or Serengeti
Search rate (km/h)	The average search rate for each trip was calculated as trip time / trip distance
Season	Seasons were defined as Short rains (November to February), Long rains (March to May) and Dry (June to October) (Sinclair 1979)
Distance	Although distance should not affect a response variable measured as predators per km, it was included as an explanatory variable for reasons explained in the cheetah sightings analysis.

All four variables were fitted to the response variable (the maximal model) and the model reduced using a backward stepwise method, removing each in turn, recording the effect on model deviance and permanently removing the variable with the lowest effect. This process was continued until all variables remaining explained a significant proportion of the data (the minimal model). The results presented firstly show the significance of all terms in the maximal model, with probability values quoted for significant terms referring to their effect on the minimal model whilst values for non-significant terms show their effect when re-added to the minimal model. Secondly, the minimal model is presented, showing the direction and strength of the average effect of each significant term. Finally, the minimal model is used to predict the actual values for a given variable whilst controlling for other significant variables. Controlled continuous variables were set at their mean value, so search rate was set at 22 km/h and distance at 95 km.

Transects

Line transects were carried out as part of a comprehensive survey of prey availability (Chapter 3), but large carnivores were also recorded when sighted. Transects were carried out in conjunction with call-in surveys, starting in July 99 and repeated every 3 months until April 2001 and surveying all three study areas, although transects in Ngorongoro were not started until July 2000. Transects were placed randomly where possible and on roads where random placement was limited by environmental obstructions and were carried out by Land Rover, driving below 20 kph and recording all sightings on either side of the vehicle. Sightings were recorded by group, estimating the number in the group and the perpendicular distance from the geometric group centre to the transect line. Analysis was then carried out using distance sampling (Buckland *et al*. 1993) and the DISTANCE software (Laake *et al*. 1998). Histograms of the data were initially examined to ensure they matched the specified shape criteria (Buckland *et al*. 1993). Data were grouped into distance intervals for analysis to remove the effect of heaping (the increased likelihood of recording convenient distances such as 100 metres as opposed to 103 or 98 metres) and truncated to remove extreme outliers if necessary. Detection functions were calculated by fitting various combinations of key and expansion terms, the best fit determined by a combination of maximum likelihood and AIC scores. Since 60-80 sightings are generally required for a good estimate of detection probability, data for each species were pooled across time and regions. The fit of the resulting detection curve was then tested using a goodness-of-fit test and if acceptable ($P>0.15$) the detection function was used to calculate estimates of group density. To calculate individual density, average group size was required. To account for the effect of distance on group size estimates, recorded group sizes were regressed against distance from the line. If the regression was significant, an adjusted group size was calculated. If non-significant, the mean was used.

Predictions of density based on prey availability

Predictions for lion, spotted hyaena and cheetah densities were calculated using estimates of prey biomass calculated using line transects analysed using distance sampling (Buckland *et al*. 1993) for each season between 1999 and 2001 (Chapter 3) and regression coefficients specific to each species as calculated by (Carbone & Gittleman 2002). Wild dogs and leopards are also listed as present in the Serengeti ecosystem but were excluded from the analysis since they were not surveyed by the call-ins or individual recognition methods and furthermore, wild dogs do not fit the general model proposed by Carbone *et al* due to their avoidance of high prey densities. Jackals were surveyed by call-ins but predictions for jackal density based on prey biomass were not made by Carbone *et al*. Four estimates for prey biomass were used to predict carnivore density. The first measure calculated all biomass, excluding no species. This measure therefore included very high peaks in biomass during periods when the migratory wildebeest and zebra passed through the area. The second measure included all species except livestock. The third measure included all species except the migrant wildebeest and zebra to examine the effect of resident species and remove the effect of the irregular peaks caused by migrants, which did not occur in all areas. (Thomson's gazelle are also migratory but retained a presence at all times throughout the year therefore were not excluded). The fourth measure excluded both migrants and livestock, leaving only wild, resident species. Since it has been shown that a single estimate of biomass for an area holds little information on prey densities due to large fluctuations in seasonal variation (Chapter 3), (McNaughton 1985) overall estimates of biomass in each region were supported by separate estimates for each region and season, controlling for annual variation and any other significant factors using generalised linear models. For further details on biomass calculations see Chapter 3.

Effort

Interview results were based on 179 interviews; 112 in Loliondo and 67 in Ngorongoro. For the sightings index, a total of 34945 km driven over 2484 hours were logged during fieldwork in all three areas representing approximately 54% of the 64600+ km driven during the study. 264 hours were spent collecting behavioural data leaving 2220 hours spent actively searching. Most kilometres and hours were logged in the Serengeti, primarily due to the fact that most journeys began from the base at Seronera. Fewest were logged in Ngorongoro, because work did not begin there until the second year. Journeys were similar in all three areas with logged trips covering a mean distance of around 96 km across about 6 hours, resulting in a mean trip search rate of about 22 km per hour (see Table 31). Search effort during line transects was high, completing over 2000 km of transects across two years in open grassland habitat (

Table 32).

Table 31- Summary of recorded trips effort

	Loliondo	Ngorongoro	Serengeti	Total
No. logged trips	100	59	208	366
Mean trip length ±SE (km)	100.7 (±5.0)	97.0 (±9.6)	92.1 (±3)	95.5 (±2.7)
Total distance logged (km)	10069.0	5723.0	19153.0	34945.0
Mean trip time ±SE (hrs)	7.0 (±0.4)	6.7 (±0.6)	5.4 (±0.3)	6.1 (±0.2)
Total time logged (hrs)	703.4	392.8	1124.0	2220.2
Mean search rate ±SE (km/hr)	17.5 (±1.0)	24.0 (±2.4)	23.6 (±1.0)	22.1 (±0.7)

Table 32 – Line transect survey effort and number of sightings (groups) of major carnivore species during 8 three-monthly surveys of grasslands, July 99-April 2001.

	No. transects	Km surveyed	No. jackal sightings	No. hyaena sightings	No. lion sightings	No. cheetah sightings
Loliondo	91	454	12	3	1	2
Ngorongoro	103	514	16	28	1	2
Serengeti	219	1117	9	38	8	4
Total	413	2085	37	69	10	8

5.4 Results

Call-ins and individual recognition

For full details on results, see chapter 4. For this study, a summary of call-in results (

Table 33) and individual recognition results (Table 34) are presented.

Table 33 – Density estimates (Ind. /km^2) based upon responses to call-ins. Average densities refer to overall density calculations for each region based on 8 survey rounds between July 99 – April 2001, controlling for all other significant influences. Minimum and maximum values refer to surveys with the lowest and highest estimates.

		Loliondo			Ngorongoro			Serengeti		
Species		Density	SE+	SE-	Density	SE+	SE-	Density	SE+	SE-
BB. jackal	Average	0.10	0.01	0.01	0.05	0.02	0.01	0.02	0.01	0.01
	Min	0.04	0.01	0.01	0.02	0.01	0.01	0.01	0.00	0.00
	Max	0.22	0.09	0.06	0.03	0.02	0.01	0.03	0.01	0.01
G. jackals	Average	0.02	0.01	0.01	0.12	0.05	0.04	0.02	0.01	0.01
	Min	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.00	0.00
	Max	0.15	0.06	0.05	0.04	0.02	0.01	0.04	0.02	0.02
Hyaena	Average	0.34	0.04	0.04	0.74	0.13	0.11	0.74	0.09	0.08
	Min	0.17	0.04	0.03	0.38	0.08	0.07	0.38	0.08	0.06
	Max	0.94	0.27	0.21	0.77	0.17	0.14	1.22	0.20	0.17
Lion	Average	0.37	0.09	0.07	0.21	0.12	0.08	0.28	0.10	0.07
	Min	0.12	0.08	0.05	0.10	0.08	0.04	0.09	0.06	0.04
	Max	0.87	0.48	0.31	0.29	0.18	0.11	0.55	0.25	0.17

Table 34 – Number of individually recognised independent (adult) cheetahs identified in each study site from photographs

	Min. number of individuals[1]	Sightings adjusted for time spent searching[2]	Density (adults/km^2)[3]
Serengeti	88	88	0.117
Loliondo	24	26	0.021
Ngorongoro	19	41	0.034

[1] Number of clearly identified individuals

[2] Since only one year was spent in Ngorongoro and Serengeti sightings included a preliminary 2 month training period, estimates for Loliondo and Ngorongoro are adjusted as if searched for the same period of time as the Serengeti.

[3] Densities were calculated based on study size areas (see chapter 2)

Questionnaire-based index

Timing of most recent sightings reported by Maasai interviewees, assumed to be representative of abundance, are shown in Figure 29 and Figure 30. The results show that, based on interviews, hyaenas were the most commonly sighted large carnivore in each region, followed by lions, leopards, cheetahs and wild dogs. However, wild dog sightings were still made relatively frequently, especially in Loliondo. Hyaenas were seen more frequently in Ngorongoro than Loliondo; lion sightings were almost identical in frequency whilst leopards and cheetahs were sighted slightly more often in Loliondo.

Figure 29 - Distribution of most recent sightings reported for each of the main carnivore species in Loliondo. All distributions were significantly different (χ^2, p<0.001) except cheetahs and leopards (χ^2_5=11.9, p=0.036).

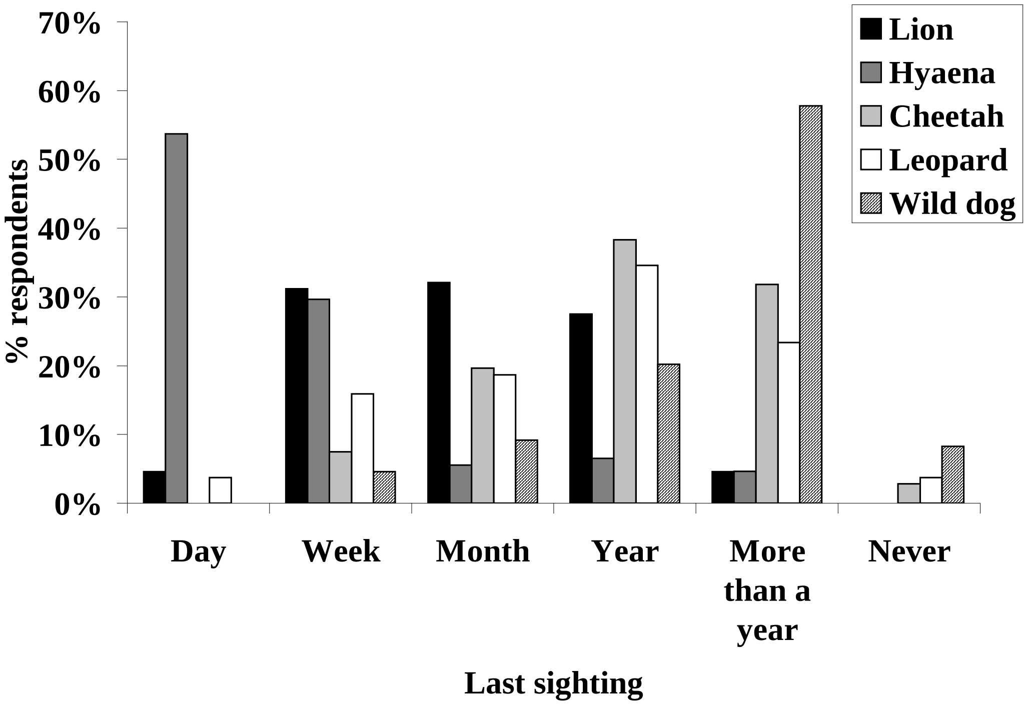
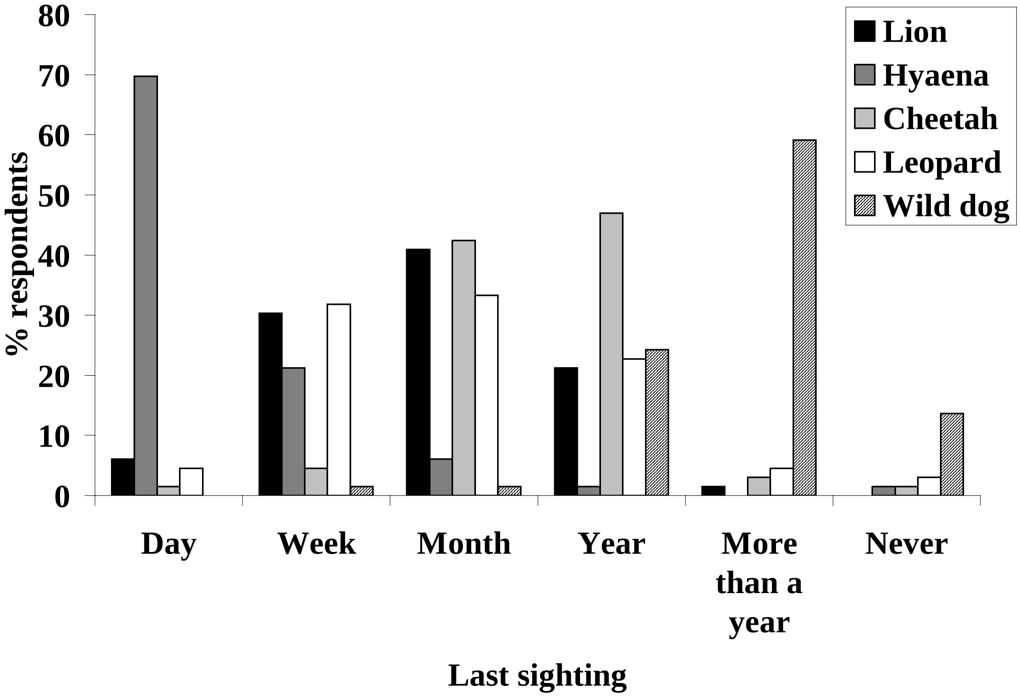


Figure 30 - Distribution of most recent sightings reported for each of the main carnivore species in Ngorongoro. All distributions were significantly different (χ^2, p<0.001).

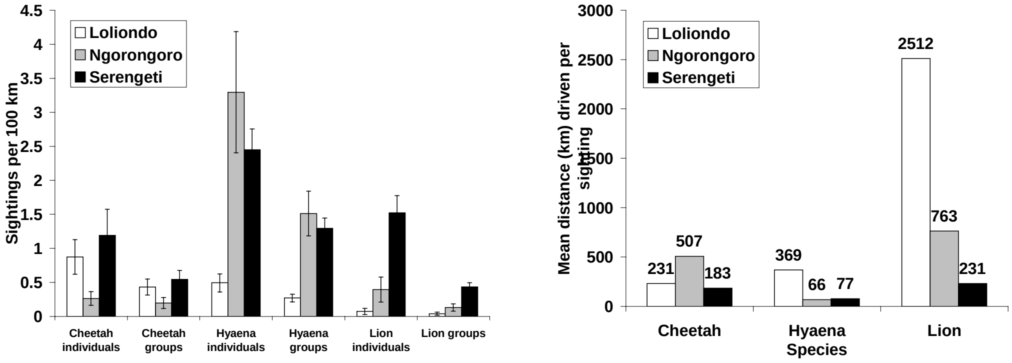


Observation-based index

Comparison of mean sighting frequencies

Comparisons of mean sightings frequencies (Figure 31) illustrate the search effort required to sight carnivores, based on a study that included a range of search rates. Sightings were particularly low outside the park, with an average of over 2500 km of daylight driving required per lion sighting in Loliondo. For a full list of all carnivores sighted, and analysis of differences in overall species richness, please see Appendix IV.

Figure 31 – Summary of carnivore sightings per 100 km logged driving. Left graph shows the mean sightings per 100 km driven (±SE). Right graph shows the mean distance required per carnivore sighting in each study area



Comparison of cheetah sighting frequencies

GLM analysis showed that sightings of individual cheetahs were significantly explained by the region searched, the season and the distance driven. Sightings of cheetah groups were affected significantly by only region and distance driven (

Table 35 and Table 36).

Table 35 – GLM results for factors affecting sightings of cheetah individuals per 100 km of driving, using Poisson errors and corrected for over-dispersion. The minimal model explained 20.6% of the total variance in the data.

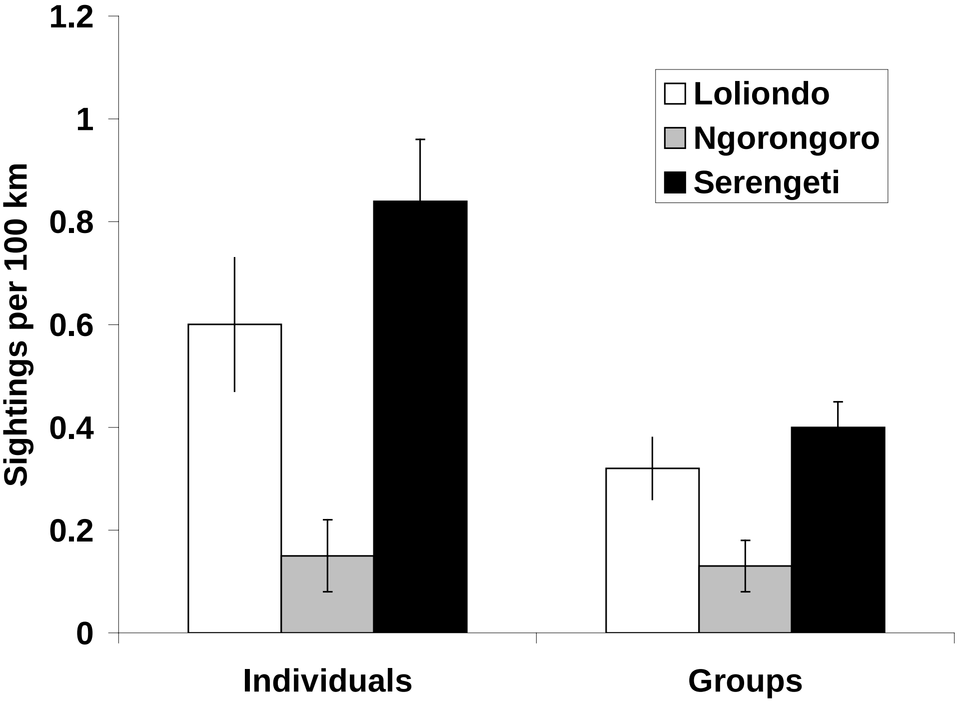
Model term	Degrees of freedom	χ^2	Probability
Distance	1	58.56	0.0000
Region	2	20.94	0.0000
Season	2	6.22	0.0446
Search rate	1	2.20	0.1383
Minimal model	Average effect		SE
Constant		1.414	0.278
Region	Loliondo	0	0
	Ngorongoro	-1.401	0.508
	Serengeti	0.34	0.229
Distance		-0.022	0.003
Season	Long dry	0	0
	Long rains	0.032	0.255
	Short rains	0.535	0.219

Table 36 – GLM results for factors affecting sightings of cheetah groups per 100 km of driving, using Poisson errors. The minimal model explained 16.9% of the total variance in the data.

Model term	Degrees of freedom	χ^2	Probability
Distance	1	53.85	0.000
Region	2	12.75	0.002
Search rate	1	1.69	0.194
Season	2	2.00	0.368
Minimal model		Effect	SE
Constant		0.705	0.244
Region	Loliondo	0	0
	Ngorongoro	-0.906	0.397
	Serengeti	0.24	0.214
Distance		-0.019	0.003

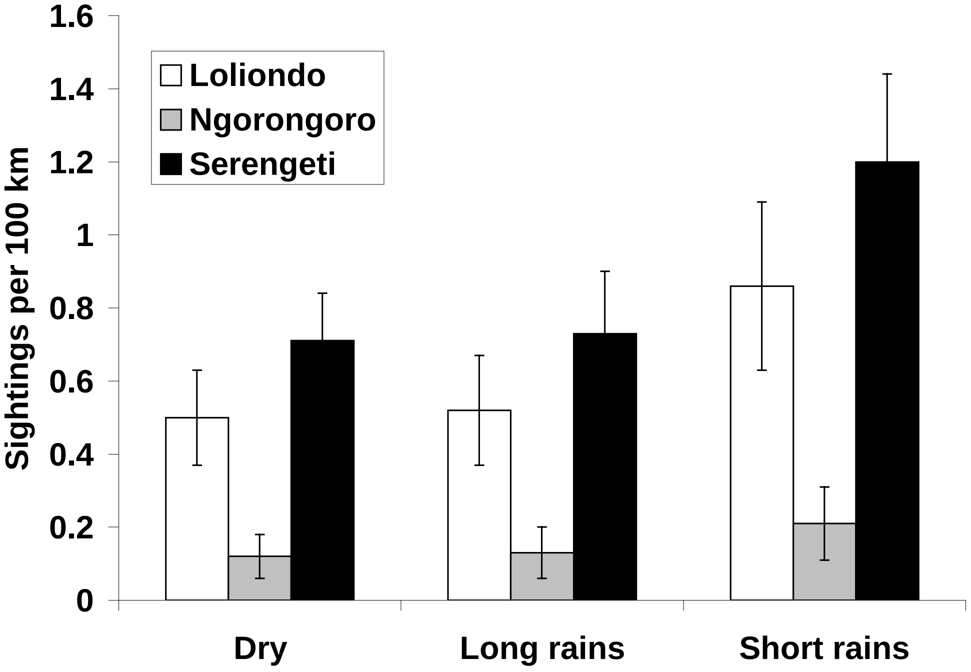
Significantly more cheetahs individuals and groups were seen whilst driving in the Serengeti than Ngorongoro (individual sightings: $\chi^2_1=21.97$, $p<0.001$, group sightings: $\chi^2_1=11.42$, $p<0.001$), however, the differences between the Serengeti and Loliondo were not significant for individuals ($\chi^2_1=1.99$, *N.S.*) or groups ($\chi^2_1=1.31$, *N.S.*). There was also significant difference between Loliondo and Ngorongoro (individuals: χ^2_1=7.78, p<0.05, groups: χ^2_1=7.21, p<0.05). The predicted effects of region, controlling for other significant terms, are illustrated by Figure 32.

Figure 32 – Predicted effect of region on cheetah individual and group sightings using the minimal model calculated using a GLM, controlling for other variables explaining a significant proportion of the data. Bars denote standard errors.



Numbers of cheetah individuals seen were also affected by season, with slightly significantly more cheetahs seen in the short rainy months (November to February) than the dry (June to October) (χ^2_1=3.58, p<0.05). However, there was no difference between the short and long rainy months (χ^2_1=2.10, *N.S.*) or long rainy and dry months (χ^2_1=0, *N.S.*) (see Figure 33). Cheetah group sightings were not affected by season, however, reflecting larger cheetah group sizes in the short rainy seasons.

Figure 33 – Predicted effect of season on cheetah individual and group sightings using the minimal model calculated using a GLM, controlling for other variables explaining a significant proportion of the data. Bars denote standard errors.



Distance also had a significant effect on cheetah individual and group sightings, with longer trips yielding fewer cheetahs per km. However, this is due to the fact that when cheetahs were spotted they were generally observed for several hours afterwards. Although this time was not incorporated into the trip time, simply spending much of the day with cheetah sightings meant that longer trips generally only occurred when cheetahs were not seen and *vice versa*. Since distance was a significant explanatory factor in explaining variation in cheetah sightings it was retained in the model and controlled for when predicting the effects of region and season. Since lions and hyaenas were not observed in the same way as cheetahs, this anomaly was unique to cheetah sighting analysis.

Comparison of hyaena sightings frequencies

The number of hyaena sightings was significantly explained by region and search rate for both hyaena individuals and groups (

Table 37 and Table 38).

Table 37 - GLM results for factors affecting sightings of hyaena individuals per 100 km of driving, using Poisson errors. The minimal model explained 14.9% of the total variance in the data.

Model term	Degrees of freedom	χ^2	Probability
Region	2	47.05	0.000
Search rate	1	16.54	0.000
Season	2	4.81	0.090
Distance	1	0.13	0.721

Minimal model		Effect	SE
Constant		-0.288	0.329
Region	Loliondo	0	0
	Ngorongoro	2.005	0.35
	Serengeti	1.727	0.328
Search rate		-0.026	0.007

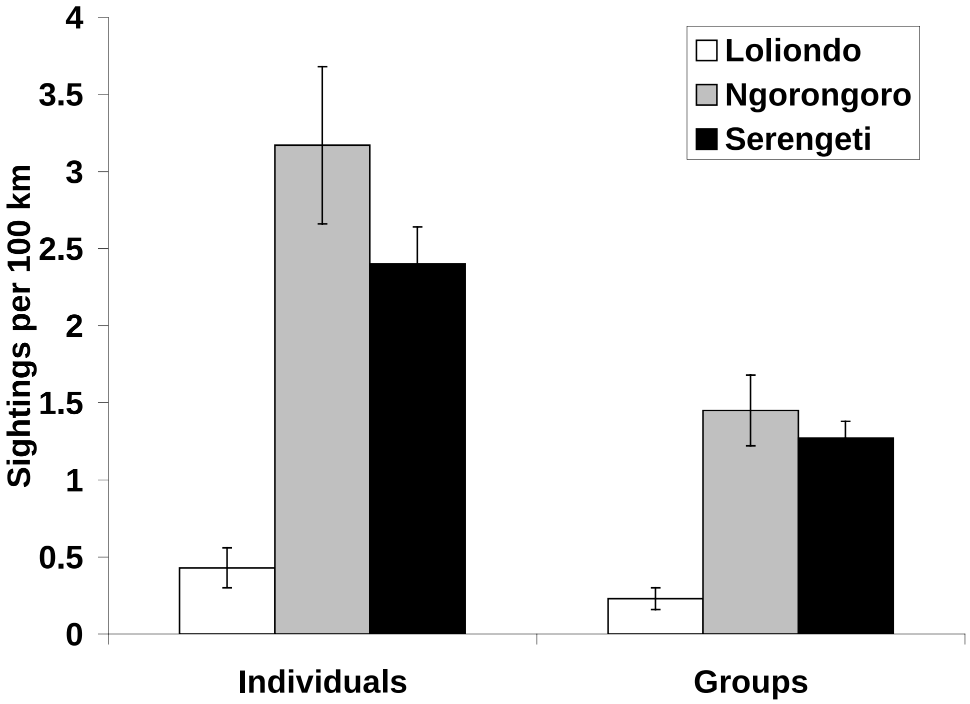
Table 38 - GLM results for factors affecting sightings of hyaena groups per 100 km of driving, using Poisson errors. The minimal model explained 16.4% of the total variance in the data.

Model term	Degrees of freedom	χ^2	Probability
Region	2	50.58	0.000
Search rate	1	20.13	0.000
Season	2	0.59	0.743
Distance	1	0.48	0.788

Minimal model		Effect	SE
Constant		-0.874	0.293
Region	Loliondo	0	0
	Ngorongoro	1.827	0.316
	Serengeti	1.693	0.291
Search rate		-0.02645	0.006

Investigating the effect of region further shows that significantly more individuals and groups were seen in the Serengeti than Loliondo (individuals: $\chi^2_1=38.84$, $p<0.001$, groups: $\chi^2_1=43.77$, $p<0.001$) but differences between Serengeti and Ngorongoro were not significant (individuals: $\chi^2_1=1.73$, *N.S.*, groups: $\chi^2_1=0.46$, *N.S.*). Differences between Ngorongoro and Loliondo were also highly significant (individuals: $\chi^2_1=43.02$, $p<0.001$, groups: $\chi^2_1=44.72$, $p<0.001$) (see Figure 34)

Figure 34 - Predicted effect of region on hyaena individual and group sightings using the minimal model calculated using a GLM, controlling for other variables explaining a significant proportion of the data. Bars denote standard errors.



Hyaena sightings were also significantly affected by search rate, particularly in the Serengeti and Ngorongoro where sightings were more frequent. Season did not have a significant effect on hyaena sightings, although sightings were slightly more frequent in the short rainy season.

Comparison of lion sightings frequencies

GLM analysis of lion sighting frequencies showed that region was the only explanatory parameter with a significant effect for either individual or group sightings (

Table 35 and Table 36)

Table 39 - GLM results for factors affecting sightings of lion individuals per 100 km of driving, using Poisson errors. The minimal model explained 15.5% of the total variance in the data.

Model term	Degrees of freedom	χ^2	Probability
Region	2	56.73	0.0000
Search rate	1	3.47	0.1768
Season	2	2.25	0.3248
Distance	1	1.41	0.4952

Minimal model		Effect	SE
Constant		-2.598	0.666
Region	Loliondo		
	Ngorongoro	1.669	0.766
	Serengeti	3.019	0.674

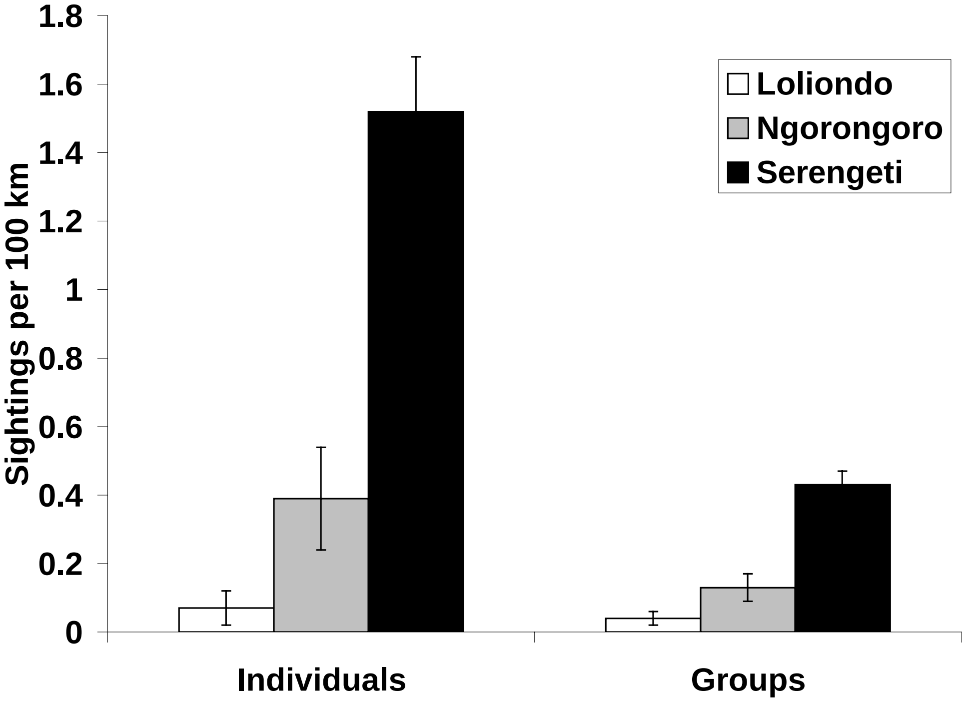
Table 40 - GLM results for factors affecting sightings of lion groups per 100 km of driving, using Poisson errors. The minimal model explained 14.3% of the total variance in the data.

Model term	Degrees of freedom	χ^2	Probability
Region	2	52.73	0.0000
Season	2	1.58	0.4541
Search rate	1	2.80	0.0941
Distance	1	0.33	0.5646

Minimal model		Effect	SE
Constant		-3.225	0.459
Region	Loliondo		
	Ngorongoro	1.194	0.569
	Serengeti	2.389	0.469

By far the majority of lion sightings of groups or individuals were made in the Serengeti and fewest in Loliondo. Differences were strongly significant for individual sightings (Serengeti-Loliondo: $\chi^2_1=194.49$, $p<0.001$, Serengeti-Ngorongoro: $\chi^2_1=58.65$, $p<0.001$, Ngorongoro-Loliondo: $\chi^2_1=19.06$, $p<0.001$). Group sightings differed strongly significantly between Loliondo and Serengeti ($\chi^2_1=46.76$) but less strongly between Serengeti and Ngorongoro ($\chi^2_1=14.24$, $p<0.05$) or Loliondo and Ngorongoro ($\chi^2_1=4.3$, $p<0.05$). The chance of sightings was unaffected by season or search rate.

Figure 35 - Predicted effect of region on lion individual and group sightings using the minimal model calculated using a GLM, controlling for other variables explaining a significant proportion of the data. Bars denote standard errors.

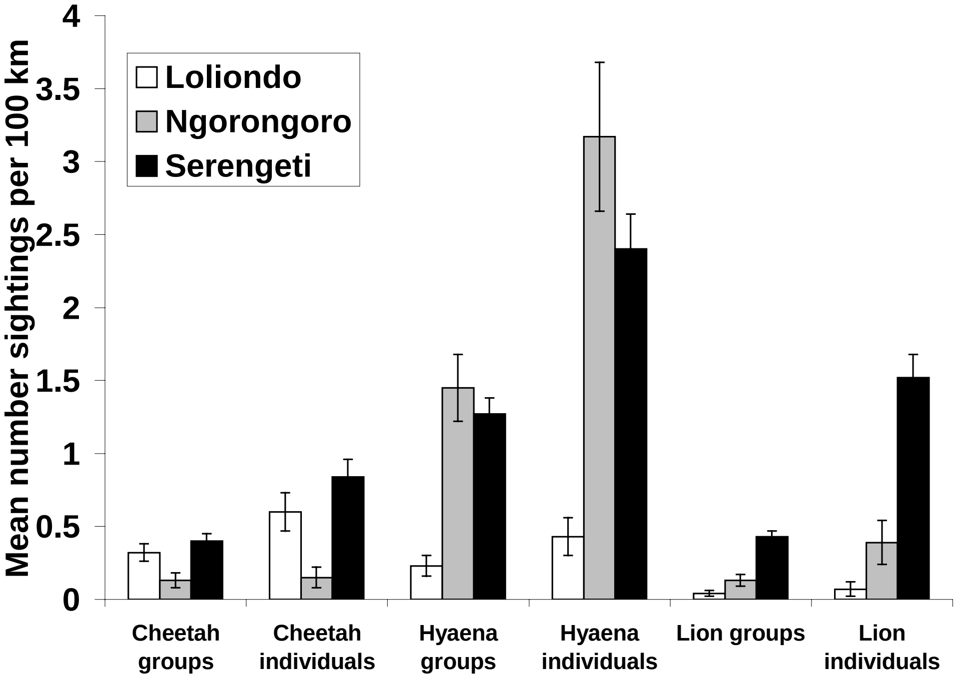


Summary of effect of region on main carnivore sightings

Since the proportion of animals sighted was unknown, the results give only estimates of relative abundance in the different study areas and provide little information on actual numbers present. Although the detected proportion is unknown and detectability can vary widely between animals, if the variation is constant across the study areas an index can present an accurate reflection of variation in the actual population (Bart *et al*. 1998), (Sutherland 1996). With these assumptions in mind, the three study sites can be compared (Figure 36 plots the previous results together for comparison). The results show that the hyaenas were the most common sighted carnivore in the Serengeti with lion and cheetah groups spotted roughly equally to one another, although more individual lions than cheetahs were seen. The pattern is similar for groups in the NCA, although hyaenas are seen even more frequently and cheetahs and lions less frequently than in the Serengeti. However, Loliondo shows completely different sighting patterns, with cheetahs the most likely carnivore to be seen whilst driving around, with hyaenas and especially lions rarely seen. Comparing each species individually shows cheetahs were seen most commonly within the National Park but non-significantly less frequently in Loliondo. The semi-protected

NCA was in fact the poorest place to see cheetahs, although cheetahs were relatively commonly sighted in all three study areas. In contrast, hyaenas were incredibly commonly sighted in the Serengeti and Ngorongoro but were approximately five times less likely to be seen in Loliondo than the Serengeti whilst lions were sighted almost fifteen times less frequently in Loliondo. If the index describes a constant proportion of the true populations it would therefore show that the populations of lions and spotted hyaenas were far smaller outside the National Park than inside, with the exception of hyaenas in Ngorongoro, where as cheetahs did not show such drastic population changes across the borders.

Figure 36 – Summary of GLM predictions for all sightings per 100 km. Bars denote standard errors.



Transects

Sighting rates were low for all species with only spotted hyaenas sighted sufficiently frequently for a relatively confident estimate of detection probability. Jackals were also fitted with a separate detection function but insufficient sightings were made for lion or cheetah sightings, therefore both were assumed to have the same detection function as hyaenas. No species was seen sufficiently frequently to allow separate detection functions to be fitted for each region, or for each survey as would be preferable in ideal conditions. Effective strip width and probability of detection was greatest for cheetahs and lowest for jackals (Table 41) although strip widths and probabilities were low for all carnivores compared to herbivore species (see Chapter 4).

Table 41 – Model choice, goodness of fit significance and parameters common across species

Species	Model	GOF (p)	Estimated strip width	CV	Probability of detection	CV
Hyaenas	Hazard rate	0.12	196	11.8	0.33	11.8
Jackals	Half normal	0.44	175	21.6	0.29	12.3
Lions	Hazard rate	0	240	5.6	0.40	2.3
Cheetahs	Hazard rate	0	265	93.9	0.44	35.5

Density of groups was calculated using the selected detection function and density of individuals calculated from the estimated group size. In all cases the regression of group size on distance was non-significant and average group size used. Since sample sizes for lions and cheetahs in particular were low, group size estimates were based on very little data and overall coefficients of variation for density estimates were high (Table 42).

Table 42 – Estimates of individual and group density and other parameters specific to each region, including degrees of freedom (Df) and coefficient of variance (CV – SE/Mean*100).

		Loliondo			Ngorongoro			Serengeti		
		Estimate	Df	CV	Estimate	Df	CV	Estimate	Df	CV
Hyaenas	Number per km	0.01	90	57	0.05	102	28	0.03	219	18
	Average group size	1.33	2	25	2.40	27	20	1.60	37	12
	Group density	0.02	98	58	0.14	134	31	0.09	279	22
	Density (individuals)	0.02	52	63	0.33	142	37	0.13	278	25
Jackals	Number per km	0.03	90	36	0.03	102	25	0.01	218	36
	Average group size	1.25	11	10	1.38	15	11	1.33	8	13
	Group density	0.08	109	38	0.09	135	28	0.02	251	38
	Density (individuals)	0.09	119	39	0.12	147	30	0.03	225	40
Lions	Number per km	0.00	90	100	0.00	102	100	0.01	218	39
	Average group size	1.00	0	0	7.00	0	0	5.90	7	35
	Group density	0.00	90	100	0.00	102	100	0.01	219	39
	Density (individuals)	0.00	90	100	0.03	102	100	0.09	35	53
Cheetahs	Number per km	0.00	90	70	0.00	102	70	0.00	218	51
	Average group size	2.00	1	50	1.50	1	33	2.00	3	29
	Group density	0.01	72	79	0.01	76	79	0.01	51	62
	Density (individuals)	0.02	11	93	0.01	31	86	0.01	42	69

Estimates of hyaena individual density were significantly higher in both Ngorongoro ($Z=20.8$. $p>0.01$) and the Serengeti ($Z=91$, $p<001$) than Loliondo and estimates from Ngorongoro were also higher than the Serengeti ($Z=12.6$, $p<0.01$). Jackal densities were also significantly higher in Ngorongoro than Loliondo ($Z=12.7$, $p<0.001$) and the Serengeti ($Z=72$, $p<0.001$) and higher in Loliondo than the Serengeti ($Z=42$, $p<0.001$). Lion densities were significantly different in all regions and highest in the Serengeti followed by Ngorongoro (Loliondo: Ngorongoro, $Z=32.17$, Ngorongoro: Serengeti, $Z=19.14$, Loliondo: Serengeti, $Z=39.8$, $p<0.001$ in all cases). Cheetahs were significantly higher in Loliondo than Ngorongoro ($Z=23.7$, $p<0.001$) or the Serengeti ($Z=25.3$, $p<0.001$) but there was no difference between Ngorongoro and the Serengeti.

Estimates from line transects therefore predict that hyaenas are the most abundant carnivore in general with the highest densities in the Serengeti and Ngorongoro. However, in Loliondo, jackals are the most abundant carnivore, followed by hyaenas and cheetahs at approximately equal densities whilst lions are effectively absent. Cheetah densities are extremely low in the Serengeti and Ngorongoro, however. Lion densities are highest in the Serengeti and rarely seen in Ngorongoro. Combined estimates for jackals also vary with region being the most abundant carnivore in Loliondo, the second most abundant in Ngorongoro and the third and relatively rare in the Serengeti.

Predictions based on prey availability

Predictions were calculated based on four measures of prey availability (total biomass including livestock and seasonal influx of migrants, biomass excluding livestock, biomass excluding migrants and biomass excluding migrants and livestock) and single regression coefficients calculated for lions, spotted hyaenas and cheetahs by Carbone and Gittleman (2002). For each measure of biomass, estimates were made for each seasonal period as well as average values, based on GLM predictions of biomass controlling for all other significant factors (see chapter 3). Standard errors for each density estimate were calculated based on standard errors for biomass calculations (Table 43 -

Table 46).

Table 43– Predictions of carnivore abundance based on total biomass (including migrants and livestock) and carnivore-prey relationships as calculated by Carbone *et al* (In press). Prey biomass estimates were derived from line transect surveys 1999-2001.

				Predicted carnivore density (Ind./km^2)					
				Lion		Hyaena		Cheetah	
Carnivores / prey[*]				0.26		0.85		1.05	
Region	Season	Prey biomass (kg/100km^2)	SE	Ind. /km^2	SE	Ind. /km^2	SE	Ind. /km^2	SE
Loliondo	Dry start	409700	196100	0.11	0.05	0.35	0.17	0.43	0.21
	Dry end	870100	273800	0.23	0.07	0.74	0.23	0.91	0.29
	Short wet	2733500	492800	0.71	0.13	2.32	0.42	2.87	0.52
	Long wet	2253100	444000	0.59	0.12	1.92	0.38	2.37	0.47
Ngorongoro	Dry start	369400	141200	0.10	0.04	0.31	0.12	0.39	0.15
	Dry end	78200	57700	0.02	0.02	0.07	0.05	0.08	0.06
	Short wet	5584400	589600	1.45	0.15	4.75	0.50	5.86	0.62
	Long wet	946800	206100	0.25	0.05	0.80	0.18	0.99	0.22
Serengeti	Dry start	106800	59000	0.03	0.02	0.09	0.05	0.11	0.06
	Dry end	763500	163700	0.20	0.04	0.65	0.14	0.80	0.17
	Short wet	426000	114000	0.11	0.03	0.36	0.10	0.45	0.12
	Long wet	568800	144200	0.15	0.04	0.48	0.12	0.60	0.15
Loliondo	Average[**]	1579500	190300	0.41	0.05	1.34	0.16	1.66	0.20
Ngorongoro	Average[**]	1763800	166000	0.46	0.04	1.50	0.14	1.85	0.17
Serengeti	Average[**]	473300	64900	0.12	0.02	0.40	0.06	0.50	0.07

[*] Predicted no. carnivores per 100 km^2 per 10000kg/100km^2 (Carbone & Gittleman, 2002)

[**] Average biomass was calculated by using a GLM to predict just the effect of region on biomass variation, controlling for seasonal variation, annual variation and any other significant factors

Table 44– Predictions of carnivore abundance based on biomass excluding livestock and carnivore-prey relationships as calculated by (Carbone & Gittleman 2002). Prey biomass estimates were derived from line transect surveys 1999-2001.

				Predicted carnivore density (Ind./km^2)					
				Lion		Hyaena		Cheetah	
Carnivores / prey*				0.26		0.85		1.05	
Region	Season	Prey biomass (kg/100km^2)	SE	Ind. /km^2	SE	Ind. /km^2	SE	Ind. /km^2	SE
Loliondo	Dry start	222400	139200	**0.06**	0.04	**0.19**	0.12	**0.23**	0.15
	Dry end	235400	139100	**0.06**	0.04	**0.20**	0.12	**0.25**	0.15
	Short wet	2313100	440400	**0.60**	0.11	**1.97**	0.37	**2.43**	0.46
	Long wet	1851600	392600	**0.48**	0.10	**1.57**	0.33	**1.94**	0.41
		1163600	158900	**0.30**	0.04	**0.99**	0.14	**1.22**	0.17
Ngorongoro	Dry start	330300	124100	**0.09**	0.03	**0.28**	0.11	**0.35**	0.13
	Dry end	62700	51000	**0.02**	0.01	**0.05**	0.04	**0.07**	0.05
	Short wet	5564100	586200	**1.45**	0.15	**4.73**	0.50	**5.84**	0.62
	Long wet	941200	201600	**0.24**	0.05	**0.80**	0.17	**0.99**	0.21
		1744000	164000	**0.45**	0.04	**1.48**	0.14	**1.83**	0.17
Serengeti	Dry start	110500	60100	**0.03**	0.02	**0.09**	0.05	**0.12**	0.06
	Dry end	763000	160900	**0.20**	0.04	**0.65**	0.14	**0.80**	0.17
	Short wet	425300	111800	**0.11**	0.03	**0.36**	0.10	**0.45**	0.12
	Long wet	567700	141500	**0.15**	0.04	**0.48**	0.12	**0.60**	0.15
		473600	63900	**0.12**	0.02	**0.40**	0.05	**0.50**	0.07
Loliondo	Average**	1579500	190300	**0.41**	0.05	**1.34**	0.16	**1.66**	0.20
Ngorongoro	Average**	1763800	166000	**0.46**	0.04	**1.50**	0.14	**1.85**	0.17
Serengeti	Average**	473300	64900	**0.12**	0.02	**0.40**	0.06	**0.50**	0.07

***Predicted no. carnivores per 100 km^2 per 10000kg/100km^2 (Carbone & Gittleman, 2002)**

****Average biomass was calculated by using a GLM to predict just the effect of region on biomass variation, controlling for seasonal variation, annual variation and any other significant factors**

Table 45– Predictions of carnivore abundance based on resident wild prey biomass (excluding wildebeest and zebras) and carnivore-prey relationships as calculated by Carbone *et al* (In press). Prey biomass estimates were derived from line transect surveys 1999-2001.

				Predicted carnivore density (Ind./km^2)					
				Lion		Hyaena		Cheetah	
Carnivores / prey*				0.26		0.85		1.05	
Region	Season	Prey biomass (kg/100km^2)	SE	Ind. /km^2	SE	Ind. /km^2	SE	Ind. /km^2	SE
Loliondo	Dry start	408900	102600	**0.11**	0.03	**0.35**	0.09	**0.43**	0.11
	Dry end	680600	125000	**0.18**	0.03	**0.58**	0.11	**0.72**	0.13
	Short wet	781100	137000	**0.20**	0.04	**0.66**	0.12	**0.82**	0.14
	Long wet	884700	147100	**0.23**	0.04	**0.75**	0.13	**0.93**	0.15
Ngorongoro	Dry start	405700	78500	**0.11**	0.02	**0.35**	0.07	**0.43**	0.08
	Dry end	98700	39600	**0.03**	0.01	**0.08**	0.03	**0.10**	0.04
	Short wet	311800	71300	**0.08**	0.02	**0.27**	0.06	**0.33**	0.08
	Long wet	387700	81100	**0.10**	0.02	**0.33**	0.07	**0.41**	0.09
Serengeti	Dry start	112600	32500	**0.03**	0.01	**0.10**	0.03	**0.12**	0.03
	Dry end	183600	39300	**0.05**	0.01	**0.16**	0.03	**0.19**	0.04
	Short wet	121900	32000	**0.03**	0.01	**0.10**	0.03	**0.13**	0.03
	Long wet	187300	40600	**0.05**	0.01	**0.16**	0.04	**0.20**	0.04
Loliondo	Average**	692600	65700	**0.18**	0.02	**0.59**	0.06	**0.73**	0.07
Ngorongoro	Average**	297800	36700	**0.08**	0.01	**0.25**	0.03	**0.31**	0.04
Serengeti	Average**	152000	18400	**0.04**	0.01	**0.13**	0.02	**0.16**	0.02

***Predicted no. carnivores per 100 km^2 per 10000kg/100km^2 (Carbone & Gittleman, 2002)**

****Average biomass was calculated by using a GLM to predict just the effect of region on biomass variation, controlling for seasonal variation, annual variation and any other significant factors**

Table 46 – Predictions carnivore abundance based on resident wild prey biomass (excluding migrants and livestock) and carnivore-prey relationships as calculated by (Carbone & Gittleman 2002). Prey biomass estimates were derived from line transect surveys 1999-2001.

				Predicted carnivore density (Ind./km^2)					
				Lion		Hyaena		Cheetah	
Carnivores / prey*				0.26		0.85		1.05	
Region	Season	Prey biomass (kg/100km^2)	SE	Density	SE	Density	SE	Density	SE
Loliondo	Dry start	234400	68400	**0.06**	0.02	**0.20**	0.06	**0.25**	0.07
	Dry end	66800	32300	**0.02**	0.01	**0.06**	0.03	**0.07**	0.03
	Short wet	333600	72100	**0.09**	0.02	**0.28**	0.06	**0.35**	0.08
	Long wet	439700	83200	**0.11**	0.02	**0.37**	0.07	**0.46**	0.09
Ngorongoro	Dry start	433000	79000	**0.11**	0.02	**0.37**	0.07	**0.46**	0.08
	Dry end	88600	35200	**0.02**	0.01	**0.08**	0.03	**0.09**	0.04
	Short wet	346300	73100	**0.09**	0.02	**0.29**	0.06	**0.36**	0.08
	Long wet	439000	83600	**0.11**	0.02	**0.37**	0.07	**0.46**	0.09
Serengeti	Dry start	109900	27300	**0.03**	0.01	**0.09**	0.02	**0.12**	0.03
	Dry end	179400	33000	**0.05**	0.01	**0.15**	0.03	**0.19**	0.04
	Short wet	125800	28300	**0.03**	0.01	**0.11**	0.02	**0.13**	0.03
	Long wet	194200	35500	**0.05**	0.01	**0.17**	0.03	**0.20**	0.04
Loliondo	Average**	267400	33200	**0.07**	0.01	**0.23**	0.03	**0.28**	0.04
Ngorongoro	Average**	323300	40200	**0.08**	0.01	**0.28**	0.03	**0.34**	0.04
Serengeti	Average**	153000	16100	**0.04**	0.00	**0.13**	0.01	**0.16**	0.02

***Predicted no. carnivores per 100 km^2 per 10000kg/100km^2** (Carbone & Gittleman, 2002)

****Average biomass was calculated by using a GLM to predict just the effect of region on biomass variation, controlling for seasonal variation, annual variation and any other significant factors**

The predictions show that large carnivores should exist outside the Park whichever measure of biomass is used, with cheetahs the dominant carnivore, followed closely by hyaenas and then lions. However, calculation of abundance varied greatly with the measure used. Based on total biomass, all densities ranged greatly, for example, hyaena estimates varying between 0.07 individuals /km^2 and 4.75 in Ngorongoro depending on when biomass was measured, but fluctuating less in the Serengeti. This was due to the uneven distribution of the migratory animals that coincided with a survey in Ngorongoro, partially coincided with a Loliondo survey and were almost completely absent during the Serengeti surveys, passing through in between (see

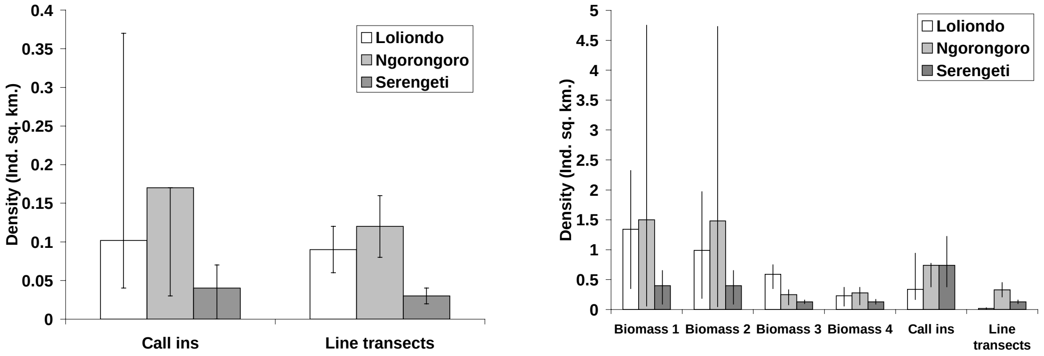
Chapter 3). Removal of livestock biomass only affected Loliondo estimates, reducing the upper and lower estimates, but removal of migrant biomass greatly reduced estimates of all carnivores and the range of estimates, although minimum estimates were reduced further outside the park. Estimates based on biomass not including migrants or livestock showed further reduced estimates, including minimum estimates outside the park. This was interesting because it showed inclusion of livestock, which were often present in seasons when wild species were absent, increased the lower estimate for carnivore abundance, which could be important since carnivores are thought to be limited by the period of minimum prey availability (Scheel & Packer 1995).

Comparison of relative and actual density estimates

Comparisons of relative abundance

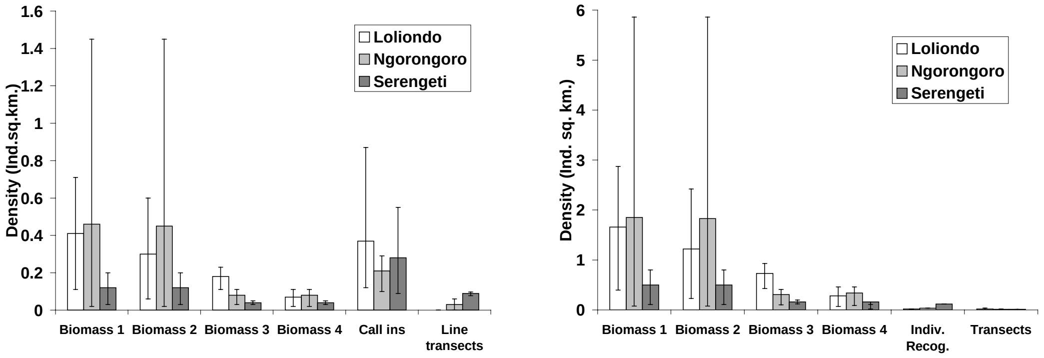
Using the different methods to compare relative abundance of carnivores a reasonable level of agreement, however, there were also some key differences when comparing between sites. Call-ins, interviews, the sightings index and line transects all agreed that hyaenas were generally the most abundant carnivore in each site. The exceptions were in Loliondo, where the sightings index and line transects both predicted other species to be more numerous, and the estimates based on biomass that always predicted cheetahs to be the most numerous. Most methods also placed lions as the next most numerous after hyaenas, with the exception of transects in Loliondo, which predicted no lions in the study area. Relative abundance of cheetahs was measured as similar to, or lower than, lions for most of the methods except biomass, which predicted cheetahs to be the most numerous carnivore.

Figure 37 – Comparisons of survey methods used for estimating carnivore abundance. Densities represent average density for each region, controlling for all other significant factors. Error bars represent minimum and maximum estimates for individual surveys or standard errors for line transect estimates[1,2]



A) Jackal density estimates

B) Hyaena density estimates



C) Lion density estimates

D) Cheetah density estimates

[1] Densities for black backed and golden jackals are combined for call-in results since line transects did not distinguish species. Densities represent average density for each region, controlling for all other significant factors.

[2]Biomass estimates were labelled as: 1=total biomass, 2= biomass excluding livestock, 3=biomass excluding migrants, 4=biomass excluding migrants and livestock, call-ins and line transects.

Comparisons of density

Comparing methods that estimated actual densities (see Figure 37 for a summary) shows the methods covering jackals predicted similar relative and actual abundance, predicting the highest numbers in Ngorongoro and the lowest in the Serengeti. Average density estimates for the whole survey period were extremely similar, although line transects predicted slightly lower densities for Ngorongoro than did call-ins, whilst the range of estimates for all call-ins was very large.

Although relative abundance estimates for hyaenas were generally in agreement, actual density estimates were not, with line transects predicting very low densities in all areas, especially Loliondo. Estimates for the Serengeti and Ngorongoro were roughly equivalent to the lowest biomass prediction and half the call-in estimates. In contrast, total biomass predicted the highest densities, higher than all call-in estimates except in the Serengeti and even with removal of migrants from the biomass the estimates were still higher than call-in estimates from Loliondo. However, use of residents only biomass gave lower estimates than call-ins in all areas and predicted densities more similar to transect results in Ngorongoro and Serengeti.

Comparisons of lion density estimations showed line transect estimates predicted extremely low densities for Loliondo and Ngorongoro whilst Serengeti estimates were similar to the lower predictions based on biomass but less than half of call-in predictions. Estimates based on total biomass were similar to call-in estimates for Loliondo, higher than call-ins in Ngorongoro and lower than call-ins in the Serengeti. However, the estimates based on the call-in survey with the most responses in Loliondo predicted higher densities than even estimates based on maximum prey availability. Removal of livestock and/or migrants from biomass estimates therefore underestimated lion densities compared to call-ins and estimates based on resident only biomass predicted similar densities to line transects in Serengeti.

Estimates of cheetah density also predicted varying population sizes, with transect density predictions extremely low in all areas, whilst estimates based on biomass were orders of magnitude higher. Individual recognition techniques were similar to transect estimates, but much lower than any of the biomass estimates.

5.5 Discussion

Within site comparisons

Within sites, the range of methods used to estimate relative abundance are not too susceptible to the method chosen within an area. With the exception of biomass, all surveys in the Serengeti predicted hyaenas to be the most abundant, lions to be next and cheetahs to be third, therefore if only a measure of presence / absence or relative abundance is required a simple index based on sightings whilst driving or interviews with locals is equally as effective as a lengthy line transect survey or call-in survey. Predictions based on prey biomass were also effective for comparing relative hyaena and lion abundance, but appeared to drastically overestimate cheetah abundance, thus bringing into question the applicability of the regression coefficients calculated by Carbone and Gittleman (2002). Although the coefficients may apply to cheetahs in theory, in practice the high level of conflict between cheetahs with lions and hyaenas (Laurenson 1994), (Durant 2000b) means that cheetah densities are generally negatively correlated with lion and hyaena density (Kelly 1998).

Estimates of actual density within sites were not as similar as relative abundance agreements, but still there was much overlap. For example, estimates of jackal densities by call-ins and line transects showed very close similarity in all three study sites. Estimates based on call-ins tended to estimate higher densities of lions and hyaenas than line transects, but were more similar to biomass estimates. Line transect estimates generally predicted the lowest densities for all species, suggesting the low visibility of carnivores might have led to many missed sightings. One unusual result was the higher densities of hyaenas predicted by call-ins than predicted by all prey biomass in the Serengeti. The fact that transect densities were closer in agreement with biomass predictions might suggest call-ins were overestimates, but most of the limitations of call-ins would be more likely to lead to underestimates (see Chapter 4). An alternative explanation could be that the Serengeti hyaenas are existing at higher levels than prey availability suggests due to the commuting system described by Hofer and East (Hofer & East 1993a) that allows populations to exceed expected limitations by travelling long distances to find food.

Comparison between sites

Although the methods chosen had strong potential to work well as survey tools if continuously applied in the same site, the same was not true of between site comparisons. In the Serengeti, the sightings index showed good agreement with other methods on relative abundance and line transects appeared to underestimate densities a little in comparison to other methods. However, in Loliondo, both line transects and the sightings-based index drastically underestimated lion and hyaena relative abundance and densities in Loliondo compared with interviews, call-ins or prey biomass estimates. Line transects did not even record a single lion in Loliondo and therefore predicted a density of 0 lions/km^2. Similar differences with other methods also occurred in Ngorongoro for lions, but appeared to still work well for hyaenas. Since call-ins showed without doubt that more lions and hyaenas were living outside the park than predicted by the sightings-based methods, even if the precise estimates were inaccurate, something must have caused the transects and sightings index to underestimate numbers. Perhaps the most likely explanation for this was variation in activity outside the park with various authors *e.g.* (Caro 1999c), (Frank & Woodroffe 2001) noting that large carnivores outside core-protected areas become more secretive and shy and would therefore be less obvious to surveys that depended on observers sighting the subjects. The fact that cheetah sightings in Loliondo did not appear to be affected to the same extent by sightings-based methods as lions and hyaenas might support this, since cheetahs are diurnal (Caro 1994) and would be restricted to the degree they could change their activity patterns, indeed it may be advantageous for them not too if it reduced conflict with lions and hyaenas.

Implications for surveying carnivores outside core-protected areas

Such results could have major implications for carnivore and other surveys comparing areas of varying protection levels. Sightings-based methods *i.e.* methods that rely on observers finding or spotting carnivores such as ground or air transect or indices of sightings from roads are still the most common technique used for rapid surveys *e.g.* Anon, 1977 (quoted in (Hofer & East 1995)), (Caro 1999b). Several studies have been published demonstrating lower density levels of wildlife, particularly carnivores, outside protected areas *e.g.* (Borner 1992), (Caro 1999d), as would this study had only line transects and a sightings index been used. Studies have been made of the comparability of carnivore surveys showing the scale of study areas, intensiveness of the techniques used and habitat variations all reduce the validity of comparisons (Smallwood & Schonewald 1998). This study supports these cautionary notes on comparability and recommends that when surveying areas with varying protection regimes it is preferable to use more than one technique, or to use methods such as call-ins that do not rely as heavily on species sightability.

Limitations of the study

Call-ins

Discussion on the limitations of estimates based on call-ins and individual recognition is provided in Chapter 4.

Interviews

Although interviews are a fairly common method for estimating abundance indices, they rely on the assumptions that a) sightings of each species are equally likely for comparison between species and b) sightings are equally biased by the effect of humans (either positive or negative) on the chance of a sightings in all areas surveyed for comparison between sites. The latter assumption might be acceptable in this case when comparing two groups of a relatively homogenous society, but in areas where people undertake a wider variety of lifestyles sightings are very unlikely to be equivalent. A pastoralist tending cattle is probably more likely to sight a lion than a farmer working in his field for example. The second assumption is probably less acceptable, with different predators probably presenting different threats to people and consequently different reactions and avoidance behaviour. However, evidence from chapter 7 suggests that, with the exception of wild dogs, all of the larger predators receive the same treatment from the Maasai.

Sightings index

Although index methods assume the proportion of animals detected within the surveyed area is unknown, the proportion is assumed to be constant with respect to factors such as region throughout the survey (Bart *et al*. 1998). There are three main factors that may have affected detection rate in the different regions that have not been controlled for in the analysis; a) habitat type, b) observer experience and c) variation in species detectability with region.

a) It can be assumed that habitats with more cover would reduce detection rates. Although the three study areas were chosen to be as comparable as possible, the areas outside the park, in particular around Loliondo, contained far more cover than on the Serengeti plains. This is exacerbated further by the fact that much of the Loliondo study area was surrounded by wooded habitat and since trips were defined only by the region in which they occurred, the portions of the journey that passed through these very low visibility habitats could not be taken into account. The Loliondo estimate in particular is therefore probably an underestimate of the index value. Since the analysis showed that cheetah numbers in Loliondo were lower than, but non-significantly different from the Serengeti estimate, the conclusion that cheetah numbers were at least equivalent in Loliondo can still be supported. Assuming the habitat bias was approximately equal for all three predator species, the extremely low hyaena and lion sightings in Loliondo might also be expected to still reflect truly low sightings, regardless of habitat. A related bias might be the use of roads and tracks, which were used more frequently in Loliondo where off-road driving was more difficult. This may have biased results to different degrees in each of the study sites, since the presence of a road can attract carnivores (*e.g.* (Mahon *et al*. 1998)) or have the opposite effect on shy species (*e.g.*(Newmark *et al*. 1996), (Maddox In prep.)).

b) Observer differences should not have had any major affect on estimates between regions since all regions were visited every month, accounting for increasing detectability with experience equally in each region.

c) The key assumption that was most likely to have been violated, and thus call-into question any conclusions on actual population sizes, was variation in species detectability, both between and within species. Such variation is very likely to have occurred when moving outside the park since the Maasai living in the NCA and Loliondo could be a likely perceived threat to carnivores (Chapter 6), thus animals outside the park would have more reason to remain hidden during daylight hours. Such differences may also have occurred between species, with the more nocturnal lions and hyaenas probably more likely to restrict themselves to night activity whilst cheetahs, generally diurnal hunters (Caro 1994), continue to be active during the day since they are not nocturnal hunters. The driving index therefore provides useful information on the effort that is required to collect data on large carnivores in the three study areas, and on the likelihood of researchers or Maasai seeing them, but these figures probably do not represent a constant proportion of the actual populations and therefore are not a reliable estimate of abundance. Instead, this index could serve as a warning to those studies that rely purely on sightings-based census techniques, such as transects, to measure carnivore density outside protected areas.

Transects

Accuracy of line transects is discussed in further detail in Chapter 3.,However, the key problem with using them for surveying carnivores was that carnivore populations were too low to get sample sizes required for accurate analysis. Even after 2000 km of transects only spotted hyaenas were seen sufficiently frequently to satisfy minimum requirements for confident detection probability calculation whilst lion and cheetah sightings were too few to be of any use. This will be due in part to low visibility leading to low strip widths and a relatively small census area and low densities in comparison to herbivores, requiring much higher effort. However, estimates outside the park were especially low, suggesting further problems with transects. One likely explanation may be the same as for the observational index: that lions and hyaenas outside the park are more wary of human persecution, therefore were not found in areas of good visibility, were inactive during the day and used hiding places to rest. This may explain why transects did appear to be relatively accurate for jackals which occurred in relatively high numbers allowing more accurate detection probability calculation and may have been more visible outside the park because the threat of human persecution was lower.

Biomass-based predictions

The accuracy of prey biomass as a prediction has been shown to underestimate known densities in some studies (*e.g.* Gros *et al*., 1996) as they rely heavily on accurate calibration from fieldwork and assume that the behavioural ecology is identical in control and study areas. However, the primary source of bias in the biomass predictions was the chosen biomass measure. As noted by McNaughton (1985) and shown in Chapter 3, a single estimate of biomass for an area as variable as the Serengeti gives little information on the ecology of prey availability. Including migrants in the estimate led to much higher average estimates with wide ranges except in the case of the Serengeti where the quarterly surveys did not happen to coincide with the bulk of the migrants passing through, thereby giving much lower predictions for carnivore density. However, estimates based on just resident biomass predicted far lower abundance than predicted by call-ins. Assuming call-ins to be a relatively accurate reflection of true abundance this would suggest carnivore populations could not be adequately predicted by resident biomass alone either.

Chapter 6: Effects of protection on aspects of large carnivore behaviour

6.1 Summary

In Chapters 3 and 4, it was established that populations of all of the major species of large carnivores in the Serengeti also existed outside the borders of the National Park. This chapter takes this comparison one step further by investigating whether these carnivore populations differ behaviourally as an result of increased threat outside the park and speculate whether the differences might represent any adaptations in carnivore behavioural ecology that help allow survival in a human-dominated landscape. This was carried out by looking at differences in activity timing, levels of vigilance and relaxation and responses to human stimuli amongst the large carnivores. Activity times for all three species were significantly different (hyaena: χ^2_{10}=38.2, p<0.001; cheetah: χ^2_{10}=29.7, p=0.001; lion: χ^2_{10}=47.5, p<0.001). A lack of evidence of active lion behaviour outside the park despite equivalent populations and observer searching time suggest that lions did indeed display reduced activity outside the park in the daytime, or at least were rarely visible. Hyaenas showed evidence of reduced activity during the day, although were still seen active, whilst cheetahs showed some signs of increased activity in the daytime, possibly exploiting the periods when their competitors were less active. No significant differences were shown in cheetah activity budgets between animals outside and inside the park (effect of region on time spent relaxed: $F_{5,65}$=0.09, *NS*) suggesting that the presence of humans in the environment had little day-to-day effect on overall cheetah activity. Responses to cowbells were mixed. Overall, cheetahs showed no significant increase in vigilance after playbacks either inside our outside the park, although lions with experience outside the park were significantly more vigilant following a playback (T_9= -2.72, p<0.05). However, no factors significantly explained the time spent vigilant or distance moved for either cheetahs or lions. Large carnivores therefore not only survive in large numbers beyond the protection of the National Park, it appears that their behaviour does not change dramatically to suit the new environment.

6.2 Introduction

Vigilance behaviour as an indicator of environmental conditions

The importance for behavioural studies in conservation biology is strongly recognised (*e.g.* see Caro, 1995) with behavioural relationships between wildlife and humans important to understand for a range of reasons; for example avoidance behaviour may facilitate coexistence whilst habituation responses may be desirable in National Parks (Whittaker & Knight 1998). In this study it is the effects of avoidance due to perceived predation risk that hold the most interest. Many studies have been carried out on levels of vigilance, defined as monitoring of surroundings (Caro 1987), as a measure of either predation risk (*e.g.* (Fitzgibbon 1989), (Fitzgibbon 1993), (Clutton-Brock *et al*. 1999), (Robinette & Ha 2001)), (Scannell *et al*. 2001), searching for resources (*e.g.* (Caro 1987), (Brown 1999), (Schaller 1972b)) or monitoring con-specifics (*e.g.* (Pusey & Packer 1994), (Treves 2000), (Robinette & Ha 2001)). Generally it is assumed that predators are vigilant for prey and prey are vigilant for predators however in some cases both options may apply (Caro 1987) and it has been argued that reasons for vigilance can be far more complex (Treves 2000). However, predation is one of the most important selective pressures for many species (Treves 2000) and generally an increasing perception of risk is thought to be represented by an increasing vigilance (Brown 1999), (Lima & Bednekoff 1999), demonstrated by an increased amount of apparently random scanning to ensure predators cannot predict periods of non-vigilance (Scannell *et al*. 2001). It might therefore be expected that if a significant increase in predation risk were exerted by human presence, large carnivores would change their behavioural patterns accordingly.

Previous studies of behavioural changes outside core-protected areas

Humans have been hunting predators since the development of stone tools (Cannon 1995, quoted in (Frank & Woodroffe 2001)) therefore it might be expected that various behavioural adaptations have evolved in response to human threats. However, research into the effects of humans on carnivore behavioural ecology is still very limited, partly because behavioural ecology is still seen as more academic than applicable to conservation and precisely because humans do affect animal behaviour. Therefore, most behavioural researchers prefer to work in core-protected areas where behaviour is “natural” (Frank & Woodroffe 2001). Nevertheless, a comprehensive review of the literature that is available is provided by Frank and Woodroffe (Frank & Woodroffe 2001). The effects of humans as known on carnivore behavioural ecology can be divided into four main sections. Firstly there is some evidence that daily behavioural patterns shift, with various informal accounts of the disappearance of large carnivores, particularly hyaenas, into thick bush during the day (*e.g.* (Frank & Woodroffe 2001), Korb, 2000 quoted in (Frank & Woodroffe 2001), S.Williams, *pers. comm.*) whilst badgers have been shown to become more nocturnal in human presence (Lindsay & Macdonald 1985). Secondly, movement patterns can alter, with red foxes avoiding areas where humans are intolerant (Lucherini & Lovari 1996) and buffalo, an important prey species for lion, showing different movement and foraging patterns in areas with humans (Hunter 1996). In a study of Brown bear populations in Anchorage, Alaska it was demonstrated that avoidance of humans facilitated coexistence (Whittaker & Knight 1998). Lions have been shown to change dispersal behaviour, rapidly moving into areas where humans have reduced previous populations, whilst hyaenas did not respond as rapidly (Smuts, 1978, quoted in Frank & Woodroffe, 2001). Thirdly, major perturbations may be caused due to changes in population structure. For example, hunted populations of lions show increased infanticide due to the increased changes in pride tenure as previous residents are removed (Whitman, *pers. comm.*), although it is also thought that lions produce more cubs in hunted areas (Creel & Creel 1997), and selection of adults, or males by hunters may also cause various knock on effects for behaviour (Frank & Woodroffe 2001). In Namibia, it is thought that cheetahs in areas with lower large carnivore densities have larger litter sizes (McVittie 1979). Finally, social behaviour may also change under human influence, with evidence of lion sociality increasing in fluidity outside protected areas (Frank 1998) and changes in copulatory behaviour and male associations shown in Zambia (Yamazaki 1996).

Changes in daily behaviour in cheetahs, lions and hyaenas in response to increased threat

Since lions and hyaenas are top predators in the core-protected areas they are generally studied in, little work has been carried out on vigilance for predators for either lions or hyaenas, with most examples looking at behaviour in relation to con-specifics *e.g.* (Pusey & Packer 1994) or prey (Schaller 1972b), (Kruuk 1972) and most behavioural changes recorded in human-affected areas refer to larger scale changes such as ranging behaviour. Daily activity changes in response to predation in cheetahs has been examined more carefully. However, these are confounded by the problem that when cheetahs are vigilant they could be either looking for predators, either carnivores or humans, prey or other cheetahs (especially territorial males (Caro & Collins 1987b)) (Caro 1987). Nevertheless, due to the strong influence of the larger carnivores on cheetah success, both through kleptoparasitism (Schaller 1972b), (Kruuk 1972), (Frame & Frame 1981), (Caro 1994) and direct predation (Laurenson 1994), (Caro 1994), (Kelly 1998), (Durant 2000b) cheetahs have been shown to increase vigilance levels in response to predation. This is particularly noticeable during vulnerable periods such as at kills (Caro 1987) or when with young cubs (Caro 1987), (Laurenson 1993) during which there are strong reactions to the presence of both lions and hyaenas (Durant 2000a). It is thought to be because of this that individuals showing stronger avoidance behaviour show consequent increases in fitness (Durant 2000b). Cheetah vigilance is therefore thought to mirror susceptibility to predators (Laurenson 1994).

Chapter aims

The aim of this chapter is to examine whether carnivore behaviour changes outside the park in comparison to carnivores inside. Investigating the full range of carnivore species and behavioural variables that could be affected by the presence of humans in the environment was beyond the scope of this project. Furthermore, restrictions on use of radio-collars meant that many aspects, such as reproductive or ranging behaviour, were impossible to measure. This chapter therefore focuses on three primary questions:

1. Does the level of diurnal activity of predominantly nocturnal large carnivores fall outside the park to reduce conflict with humans? Does this give an advantage to the diurnal cheetahs?
2. Are daily activity patterns different outside the park, with individuals spending less time relaxed and more time alert to enable avoidance of the added threat of humans? Assuming vigilance due to prey searching is equivalent is there any evidence for increased vigilance due to perceived predation risk?

3. Do carnivores outside the park react negatively and more strongly to a human stimulus than carnivores inside the park?

6.3 Methods

Diurnal activity

Diurnal activity was analysed by taking a random sample of predator sightings at different times of the day inside and outside the park, and investigating whether each species was more or less likely to be active at different times of the day. The sightings were obtained from the predator sightings dataset, whereby every time a large carnivore was sighted during work or travel in the Serengeti ecosystem the species, location, time of day and activity was recorded. Only sightings made by the author whilst driving or carrying out transects were included in the analysis. For further details on the predator sightings dataset please see Chapter 3. Activity for each sighting was defined as the behaviour in progress when the observer arrived (*e.g.* if a hyaena got to its feet as the vehicle passed it was described as lying). For the purpose of this analysis, activities were then amalgamated into two categories; active (standing, walking, running, hunting or any other behaviour involving movement) or inactive (sitting or lying) and time was amalgamated into six time periods; 1 (before 07:00), 2, (07:00-09:00), 3, (09:00-12:00), 4, (12:00-15:00), 5 (15:00-17:00) and 6 (after 17:00). The proportion of sightings seen during each time period that were active was then calculated and plotted.

Cheetah sightings and behavioural focals

Due to limitations on time, detailed behavioural focals were only carried out on cheetahs. These were carried out whenever possible following a cheetah sighting (see Chapter 3 for details on cheetah search protocol) and generally lasted a minimum of one hour, with many focals outside the park lasting considerably longer. Before any data were collected on current behaviour, a variety of potentially influential factors were recorded. These included details on the cheetah age (only independent cheetahs were focal-followed – these were classed as young adults if their neck was still fluffy or old adults if not), sex, belly size and tameness, both recorded on a scale of 0-5 (Table 47), presence or absence of cubs and the time period behaviour recording was started.

Table 47 – Scales used to describe recent feeding behaviour and tameness

Score	Belly size	Tameness
0	Starving	Can approach within 15m
1	Very thin	Move off 30-15m
2	Usually hunting	Move off 30-50m
3	Medium	Move off 50-500m
4	Recently eaten, swollen	Hide, then run if approached
5	Just eaten. As if a basketball has been swallowed	Move off if approached within 500m+

To enable recording of a continuous variable such as behaviour, cheetah activity was classified into 21 behaviour types based on advice of previously recognised categories (S. Durant, *pers. comm.*), (Caro 1987) with the full list of classifications presented in the appendix. Commonly, behavioural data are collected through regular scans (*e.g.* (Caro 1987), (Durant 2000a), (Robinette & Ha 2001)). However, in this study continuous data were collected using the methods of Clutton-Brock *et al* (Clutton-Brock *et al*. 1999), using a Psion LZ60, which was programmed to assign each key to a different behavioural type whilst timing with an internal clock. The observer could therefore press the appropriate key each time the behaviour changed, allowing the duration of every behaviour type to be recorded to the nearest second and no assumptions of the representative value of scans were required. Transitions between behaviour types were generally clear, therefore accuracy of timing should be high. However, for simplicity, only the ten most common behaviour types were used in this analysis (Table 48, Figure 38). These categories accounted for an average of 98.1% of cheetah activity in each focal. Furthermore, analysis was also carried out on two amalgamated behaviour types, also described in Table 48. In all cases the proportion of time spent carrying out an activity was analysed rather than the rate, following the previous work of Caro (Caro 1987) and Durant (Durant 2000a).

Table 48 – Eleven predominate behaviour types used in analysis. The categories accounted for over 98% of cheetah behaviour.

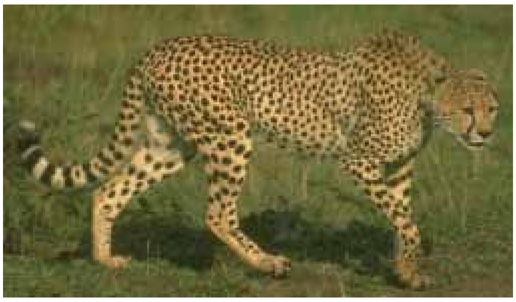
Classification	Description
Lying prone (LP)	Lying with the shoulders and head on the ground. The most relaxed form of behaviour with little possibility of spotting predators or prey.
Lying prone, head up (LHP)	As above but with the head up. Cheetahs often dozed in this position.
Lying, head up (LH)	Lying with the shoulders and head off the ground
Lying	Used when cheetah is definitely lying down but its exact position is not visible (*e.g.* in long grass)
Sitting	Hindquarters in contact with the ground
Standing	Hindquarters not in contact with the ground
Walking	The usual form of movement
Trotting	A distinct, faster gait than walking. Often used when initially approaching prey from a distance or moving away from a more distant threat.
Washing	Usually carried out when LHP or LH
Stalking	A distinct posture and walk used for approaching prey. Shoulders appear hunched, head is lowered. Movement occurs in spurts, freezing when the target looks up.
Relaxed	Amalgamation of all time spent in any lying position or washing.
Moving	Amalgamation of walking, trotting or running time.

Figure 38 – Examples of cheetah behaviour categories

a) Lying head up (LH)

b) Sitting

c) Standing **d) Stalking**

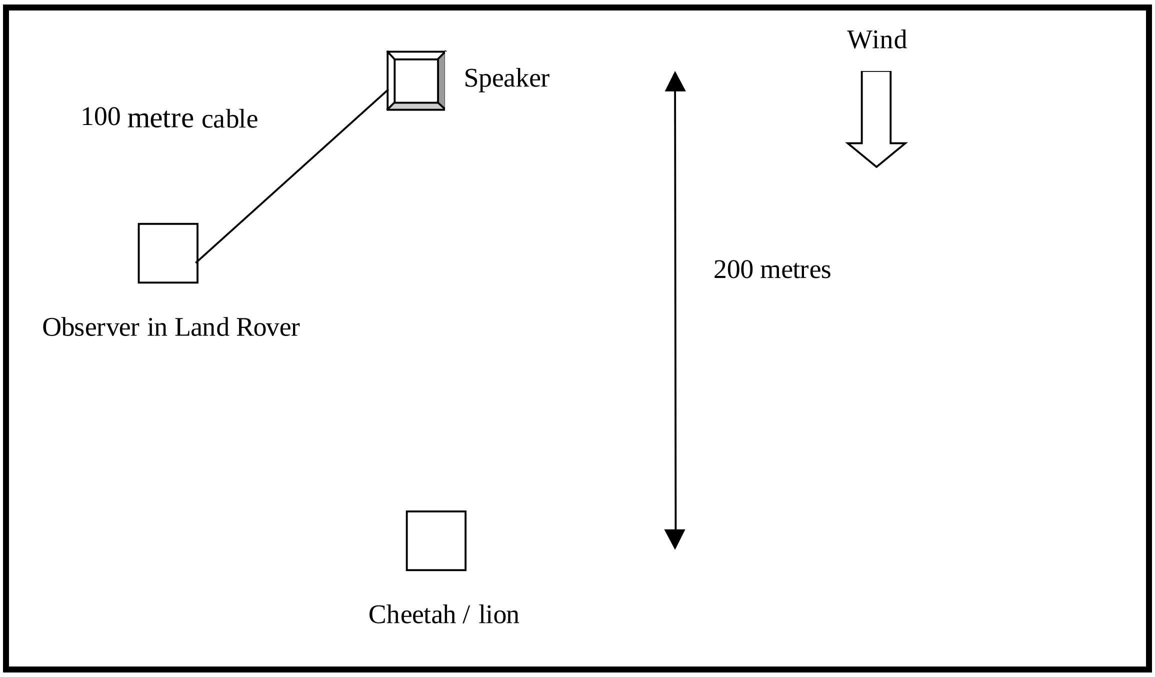


Response to human stimuli

Responses to human stimuli were tested in cheetahs and lions by playing recordings of Maasai cattle herds in which neutered males wear distinctive sounding metal cowbells similar to those in the European Alps. Playbacks have been used to test behavioural responses to specific cues for a variety of species, including insects (Jones *et al*. 2002), amphibians (Grafe *et al*. 2002), birds (Nagle *et al*. 2002), rodents (Randall & Rogovin 2002), primates (Semple 1998), (Wich *et al*. 2002) and carnivores (McComb *et al*. 1993), (McComb *et al*. 1994), (Durant 2000a), (Grinnell & McComb 2001). In this case, four recordings of cattle and their herders were made, all using a Sony TCD3 Digital Audio Tape-Corder and a Stennhauser gun microphone. One recording was made in Ngorongoro and three in different areas of Loliondo. Herd sizes were all roughly the same size (approximately fifty animals) and were all slowly moving when recorded, giving a near-continuous cowbell sound. Recordings varied primarily in the frequencies of cows lowing or herders whistling. The peak sound pressure at 1 metre was measured for each herd during recording.

Playbacks were then carried out whenever possible to cheetahs and lions both inside and outside the park. Playbacks were carried out at any time of the day (since Maasai cows could theoretically be encountered throughout the day) but were not carried out on individuals that had moved in the previous ten minutes, looked likely to move in the near future, or showed any interest in hunting to try and ensure that any response behaviour recorded was most likely to be due to the playback. Playbacks were carried out using the same DAT player used for recording, a Sony XM 4020 amplifier and a single 150W Martin Audio studio monitor loudspeaker. Following the methodology used by McComb for playbacks to lions (McComb *et al*. 1994), the speaker was placed 200m (measured using either the vehicle odometer or GPS) from the subject (at least 75m has been recommended in previous studies (Waser, no date)), with the speaker preferably obscured by vegetation and the wind blowing towards the subject to reduce the chance of the subject not hearing the recording. The speaker was then attached to the amplifier with a 100 metre cable and the observer drove back towards the subject at an angle allowing responses to be recorded at a closer distance and ensuring any response was to the speaker, not the vehicle (Figure 39).

Figure 39 - Cowbell playback set up



Wind speed (low - <3m/s, medium – 3-5m/s, high – 5m/s+), direction (towards subject / crosswind), speaker visibility (visible / not visible) and local habitat (open / closed) were noted and ten minutes of pre-playback behaviour (Waser, no date) were then recorded (as described for recording activity budgets, above) with the subject's approximate GPS location and distance to the speaker recorded every five minutes. A randomly chosen cowbell recording was then played at a volume giving an equal decibel output at 10 metres from the speaker to the original decibel level noted when recording the cattle (generally around 70-80 dB). The recording was played for 2 minutes and the subject's actions recorded continuously for a total of one hour following the start of the tape (*i.e.* pauses to record location were not counted in the hour). Location records were also continued every five minutes from the beginning of the experiment and the subject followed slowly by car if it moved. To gauge more subtle responses to the recording, it was also continuously noted whether the subject was looking in the direction of the speaker, in addition to the primary behaviour classification such as sitting, standing *etc*. The only exception to this data collection protocol occurred with some lions. When groups of cheetahs were tested only the response of a single adult was observed. Since lions were frequently in groups of several adults where the response of more than one member was of more interest, many playbacks were recorded on paper, focal-following a single adult as per cheetahs but also attempting to monitor other members of the pride. Since continuous observation of a single individual was impossible whilst also observing other individuals, responses to these playbacks were recorded as the behaviour at one minute snapshots. If the focal lion was seen looking at the speaker at any time in the previous minute, it was recorded as looking at the speaker. In this analysis, only the responses of the single, focal-followed member of any lion group is used (in general, groups either all responded or all did not respond anyway) and all responses are presented as the proportion of time spent carrying out a given behaviour type. However, the continuous data recorded from cheetahs are likely to be more precise then the scan-based method used for most lion playbacks.

In addition to cowbell playbacks, a number of control playbacks were also carried out to ensure that responses were specific to the sound of Maasai and not simply a result of cheetahs in a given area being more nervous of noise in general. Playback protocol and volume were identical to cowbell playbacks but selection of the sound to be played took more consideration. Much debate exists over the choice of control playbacks (*e.g.* (Semple 1998)), with uses of silence (Durant 2000a), “white noise” (a tape with no sound) (Semple 1998), classical music as a control for bird calls (Forsman & Monkkonen 2001), bird calls as a control for rodents (Randall & Rogovin 2002), and both same species and various man-made noises as controls for primates (Waser, no date). In this case, the control sound needed to be a natural noise so as not to represent humans in any way, but species present in the Serengeti were avoided on the off chance their calls may mean something to Serengeti carnivores. Furthermore, any sounds that may contain universal information, such as alarm calls or distress calls, were avoided. In the end, birdcalls were settled upon as a relatively non-intrusive sound used successfully in other studies (Randall & Rogovin 2002). A recording of king penguins was chosen from a collection of southern African birdcalls. Since the calls were recorded from a large group of birds calling simultaneously it was thought unlikely that they were alarm calls. It was also felt to be fairly unlikely that either cheetahs or lions would be familiar with penguin calls!

Analysis

Analysis of diurnal activity was carried out on the actual frequencies of active sighting for each species at each time period in each of the study regions. Frequencies were then compared statistically using a χ^2 contingency table.

Analysis of activity budgets was carried out using multiple regressions and generalised linear models, enabling the effect of being inside or outside the park to be investigated whilst controlling for other potentially significant factors. Using a behaviour category or amalgamated category as the response variable, the data were first tested for normality and transformed if necessary. If the response variate could not be normalised, binomial errors and logit link functions were fitted as appropriate for proportional data (Crawley 1993). The maximal model was then built by fitting the cheetah location, tameness, sex, age, time of day, belly size and presence or absence of cubs to the response variate and removed sequentially until only significant variables remained.

Before analysis, cheetahs and lions used in the analysis were divided into categories of exposure to humans depending on their known history. For cheetahs, this allowed all subjects tested within the Serengeti to be divided into individuals unlikely to have ever ranged outside the park and individuals that had been seen outside the National Park, or whose ranges were known to extend to at least the edge of the National Park (*S. Durant, pers. comm.*). For all other cheetahs, and all lions, the category was determined by the location of the playback (Table 51). Two types of analysis were then carried out on playback data. Firstly, the presence or absence of a response was analysed in each area and for cowbells and control playbacks by comparing the mean proportion of time spent a) vigilant b) looking at the speaker and c) moving from the speaker before and after the playback, applying a standard paired t-test if data could be normalised. If transformation was unsuccessful, comparisons were made using the non-parametric Wilcoxon matched pairs test. Secondly, the factors affecting any response were investigated, primarily to determine the effect of being inside or outside the park whilst controlling for other potentially explanatory factors. This was carried out by using multiple regression techniques, fitting various potential explanatory factors and variables to proportional measures of responses, distances moved in relation to the speaker, and the latency before any movement occurred. Data were transformed where possible before analysis using an arcsine transformation for proportional measures and logarithms for distances and latency. When transformation was unsuccessful, analysis was continued as a Generalised Linear Model (see Chapter 2 for details), specifying appropriate error structures (Crawley 1993). All models were reduced to only their significant components in a reverse stepwise fashion.

All transformations of proportional data in all analyses were carried out using an arcsine transformation; all other transformations were carried out using natural logarithms, adding 1 to raw data if zeros were present (Zar 1999). Tests for normality were carried out using Kolmogorov-Smirnov (K-S) tests. Normality was assumed if the tests showed the data to be non-significantly different from normal ($p>0.05$ unless stated otherwise).

Sample sizes

Diurnal activity

Of the large predators recorded during the study suitable for analysis of activity, most were within the National Park. Lions sightings in particular were poorly represented at certain times during the day outside the park (see

Table 49).

Table 49 - Number of large predator individuals seen by driving or transects at different times of the day, with activity recorded

Region	Time period	No. sightings		
		Cheetah	Hyaena	Lion
Loliondo	Before 07:00	0	5	0
	07:00-09:00	4	6	1
	09:00-12:00	7	4	1
	12:00-15:00	2	1	0
	15:00-17:00	7	0	0
	After 17:00	5	9	8
Ngorongoro	Before 07:00	1	0	2
	07:00-09:00	1	49	0
	09:00-12:00	1	20	0
	12:00-15:00	0	16	0
	15:00-17:00	0	6	0
	After 17:00	1	17	2
Serengeti	Before 07:00	4	59	1
	07:00-09:00	27	86	25
	09:00-12:00	10	46	2
	12:00-15:00	0	31	6
	15:00-17:00	2	21	6
	After 17:00	1	53	3
Total		73	429	57

Cheetah activity budgets

100 behavioural focals were carried out on different cheetah sightings totalling nearly 140 hours. The only category for which no data were obtained was adult male cheetahs in Loliondo.

Table 50 – Total effort (hours) of intensive behavioural data collection from cheetahs

		Number of focals / total time (hrs)			
Age	Sex	Loliondo	Ngorongoro	Serengeti	Total
Adult	Female	14 / 23.5	6 / 13	36 / 51	56 / 87.5
	Male	0 / 0	2 / 1.2	7 / 11.5	9 / 12.7
Young adult	Female	1 / 4.8	1 / 1.2	18 / 19.4	20 / 25.5
	Male	1 / 2.1	1 / 0.5	13 / 11.4	15 / 14
Total		16 / 30.4	10 / 15.9	74 / 93.4	100 / 139.7

Cowbell playbacks

Sixty playbacks were carried out, nearly two thirds of which were tested on cheetahs. Most were carried out within the park since subjects outside the park were frequently too intolerant of the activity required to set up a playback experiment (Table 51).

Table 51 – Sample effort for cowbell and control playbacks

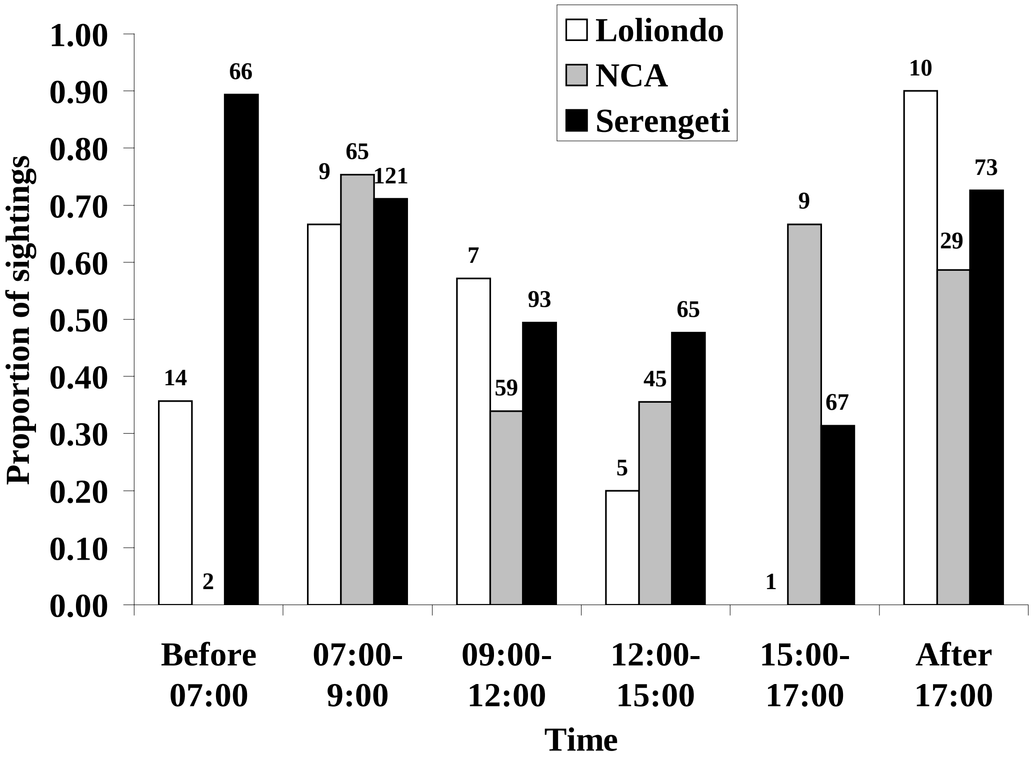
Category	Playback type	Cheetahs	Lions
Serengeti, no known experience outside park	Cowbells	11	8
	Control	1	2
Serengeti, likely experience outside the park	Cowbells	15	-
	Control	0	-
Loliondo	Cowbells	6	4
	Control	1	2
Ngorongoro	Cowbells	4	6
	Control	2	0
Total		38	22

6.4 Results

Diurnal activity

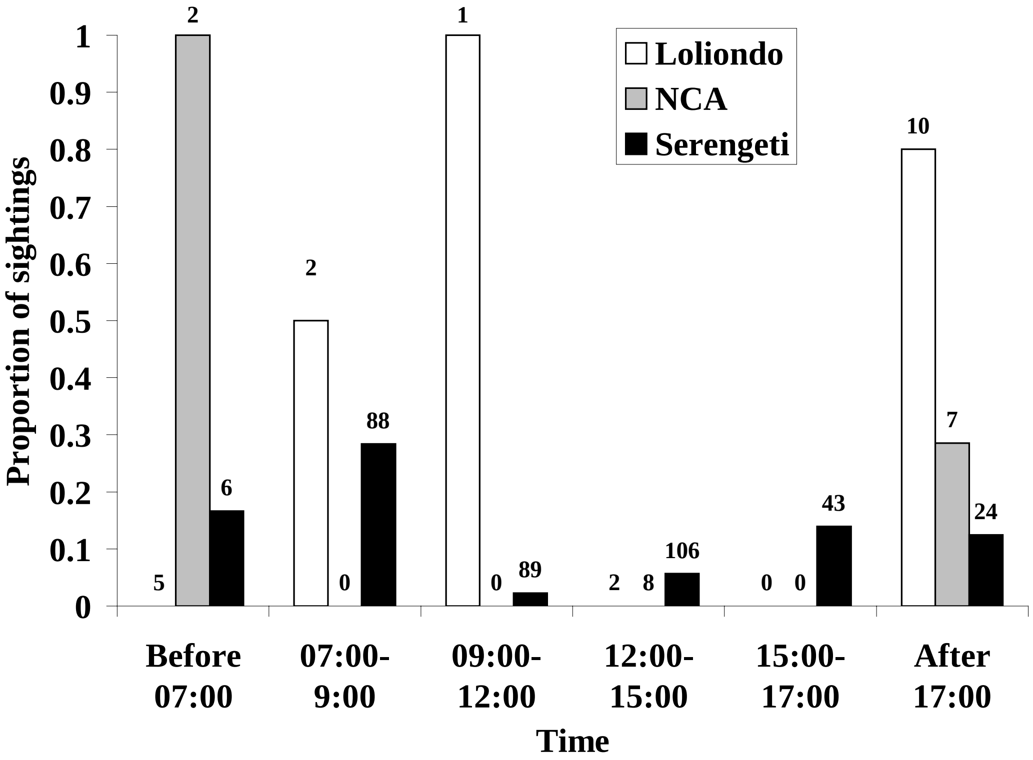
In general, sightings of all three of the large predator species were more likely to be active during the early and late segments of the day and least likely to be active during the middle of the day. Plotting the proportions of sightings that were active against time therefore results in a roughly U-shaped curve when sample sizes are adequate (Figure 40- Figure 41). However, frequencies of activity at different time periods in each region were significantly different for each species (hyaena: χ^2_{10}=38.2, p<0.001; cheetah: χ^2_{10}=29.7, p=0.001; lion: χ^2_{10}=47.5, p<0.001). By comparing the graphs, the main areas of difference can be identified.

Figure 40 – Proportion of hyaenas seen in each area that were active (standing, walking or running) when sighted at different periods of the day. Numbers above the columns show sample sizes.



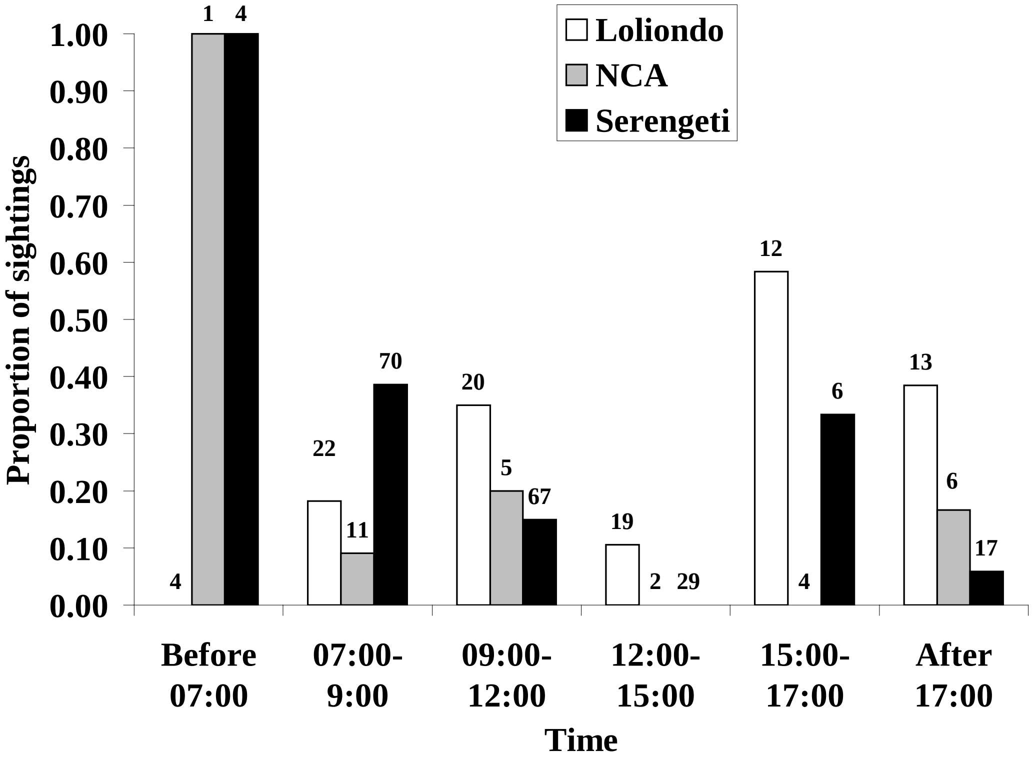
For hyaenas, activity tended to be less frequent amongst sightings between 09:00 and 17:00 in all three regions. The exact pattern of activity level differed slightly inside and outside the park, with Loliondo activity falling to the lowest level, Ngorongoro falling to a medium level and Serengeti hyaena activity remaining the highest during the low period, suggesting some support for the hypothesis that animals outside the park would be less diurnal. However, in contrast to the hypothesis, hyaena activity was still relatively high even at the middle of the day in all three regions. Furthermore, if the earliest and latest time periods were excluded from the analysis, the differences between regions between 07:00 and 17:00 were not significant (χ^2_6=3.46, p=0.749). The primary differences therefore appeared to be in the early morning, with hyaenas outside the park being particularly inactive compared to those in the Serengeti, although sample sizes outside the park were too low for statistical comparison. Finally, general levels of activity for hyaenas were high throughout the day, with an average of 58% of hyaena sightings being active and no time period with a sample size of more than 10 showing activity levels below 30%.

Figure 41 – Proportion of lions seen in each area that were active (standing, walking or running) when sighted at different periods of the day. Numbers above the columns show sample sizes.



The general pattern of lion activity in the Serengeti again showed a roughly unimodal U-shape, with activity higher earlier and later in the day and the lowest periods between 09:00 and 15:00. Activity was generally much lower than hyaenas with just 15% of sightings being active. Statistical comparisons between the regions are impossible due to the low sample sizes outside the park. However, it is significant to note that in the over two years in the Serengeti, active lions were seen throughout the day. In contrast, outside the park in Loliondo only one active lion was sighted between 09:00 and 17:00 (and she was sighted close to the park boundary) during the two years, despite census surveys showing an equivalent population density outside the parks (Chapters 4 and 5).

Figure 42 – Proportion of cheetahs seen in each area that were active (standing, walking or running) when sighted at different periods of the day. Numbers above the columns show sample sizes.



In contrast to the lion and hyaena activity patterns, cheetah activity in the Serengeti and Loliondo generally followed a bimodal distribution, with peaks between 07:00 and 12:00 and after 15:00. Patterns in Ngorongoro could have been similar but were impossible to determine with confidence due to the low sample sizes. Activity levels were relatively low compared to hyaena sightings, with 23% of sightings being active. Comparisons between regions were again restricted by low sample sizes but sightings before 07:00 suggested that cheetahs in Loliondo were less likely to be active whilst sightings inside the park were all active whilst sightings between 09:00 and 17:00 tended to be more active in Loliondo than inside the park.

Cheetah activity budgets

Cheetah behaviour was reduced into ten categories, the nine activities accounting for most of the cheetahs' time and a tenth category incorporating all other behaviour (eating, drinking *etc*.). Initial plots of the overall proportion of each focal that were accounted for by each behaviour category show little difference in activity budgets in each of the three regions (Figure 43). However, the time spent on different behaviours is likely to vary with age, sex, the time of day and other factors. Three key behaviour categories were therefore regressed against a range of potential explanatory factors to determine whether region alone accounted for any variation. The chosen measures of behaviour were the proportion of each focal spent “relaxed” (a combination of time spent in any of the four lying positions together with time spent washing), the proportion of time spent moving (a combination of time spent walking, trotting or running) and the proportion of time spent lying prone. The latter was chosen since lying prone appears to be the most vulnerable form of behaviour; the cheetah has its head at ground level with no opportunity for scanning its environment and usually the eyes are shut.

Figure 43 – Average activity budgets for all cheetahs focal-followed in each region

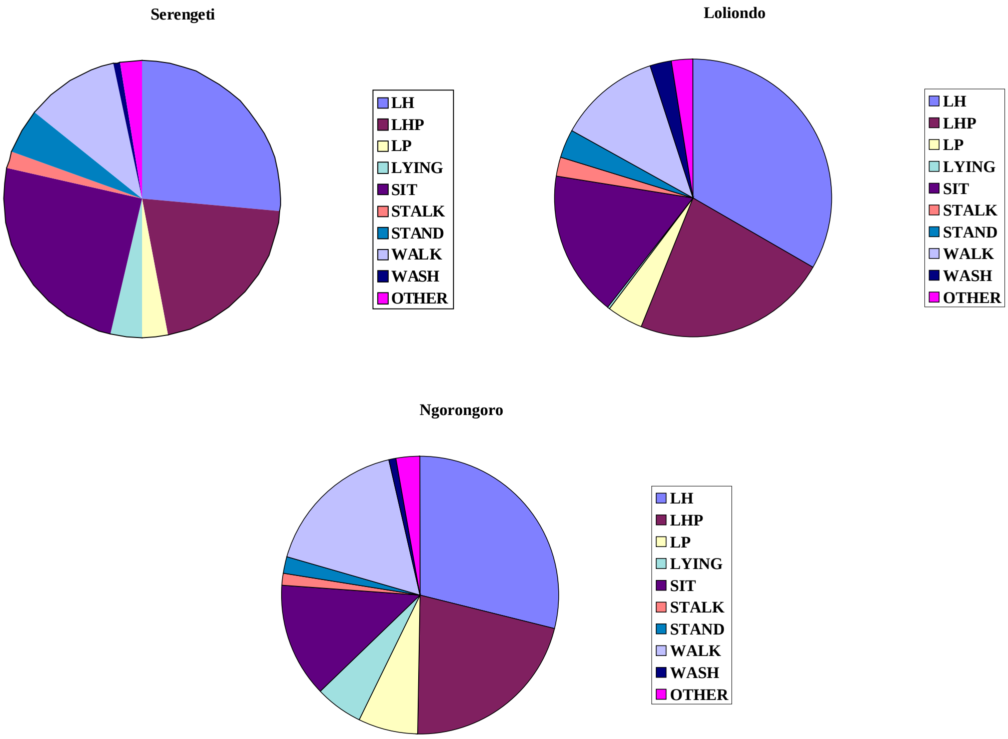


Table 52 – Factors affecting proportion of time spent "relaxed" (all lying positions plus washing combined) and moving (walking, trotting and running combined)

		Coefficient	Statistic	Significance
Proportion of time spent relaxed				
Constant		1.036		
Time	1 (< 07:00 / > 17:00)	0	$F_{1,69}$=3.25	P=0.026
	2 (07:00-09:00 / 15:00-17:00)	-0.539		
	3 (09:00-15:00)	-0.627		
Age	Adult	0	$F_{2,68}$=13.03	P<0.001
	Young adult	0.373		
Region		-	$F_{5,65}$=0.09	P=0.911
Cubs present		-	$F_{4,66}$=0.29	P=0.590
Tameness		-	$F_{4,66}$=0.00	P=0.948
Sex			$F_{4,66}$=0.22	P=0.640
Belly size		-	$F_{4,66}$=0.82	P=0.370
Region.Time		-	$F_{8,62}$=2.47	P=0.071
Region.Age		-	$F_{8,62}$=0.38	P=0.687
Region.Sex		-	$F_{6,64}$=1.85	P=0.178
Proportion of time spent moving				
Constant		0.286		
Age		-	$F_{2,68}$=3.54	P=0.064
Belly size		-	$F_{2,68}$=1.02	P=0.315
Cubs present		-	$F_{2,68}$=0.02	P=0.894
Region		-	$F_{3,67}$=0.30	P=0.742
Sex			$F_{2,68}$=0.76	P=0.386
Tameness		0.093	$F_{0,70}$=5.11	P=0.027
Time		-	$F_{3,67}$=0.96	P=0.387
Region.Age	Ngorongoro, young adult	0.978	$F_{6,64}$=3.34	P=0.042
	Serengeti, young adult	0.254		
Region.Time		-	$F_{8,62}$=1.62	P=0.193
Region.Sex		-	$F_{5,65}$=1.00	P=0.322

Figure 44 – Effect of region on activity. Graph A shows the predicted effect of region (±SE) on proportion of time spent relaxed, controlling for the effects of time and age which were significant. Graph B shows the significant interaction between age and region (±SE) on time spent moving. Variation attributed to region alone was not significant for either model

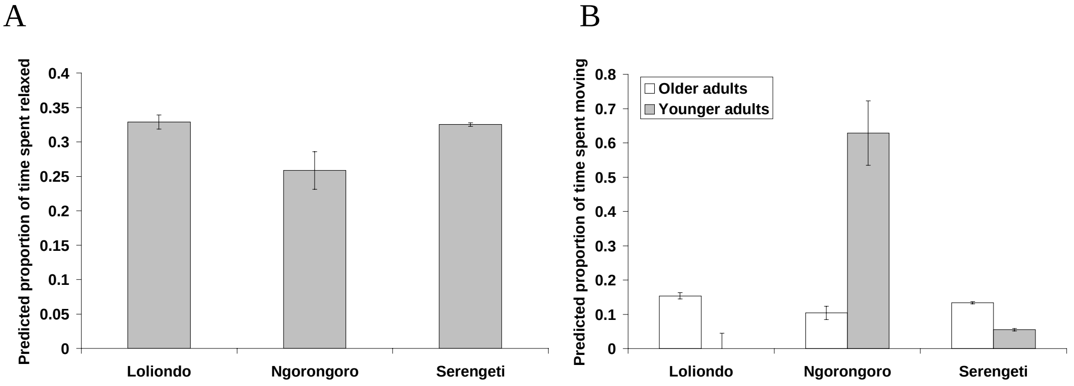


Table 53 – GLM results[1] for factors affecting the proportion of time cheetahs spent lying prone, the most relaxed and vulnerable behaviour category. No factor was significant.

Factor	Coefficient	Statistic	Significance
Age	-	$\chi^2_1=2.82$	P=0.093
Belly size	-	$\chi^2_1=0.35$	P=0.554
Cubs present	-	$\chi^2_1=1.01$	P=0.315
Region	-	$\chi^2_2=0.36$	P=0.835
Sex	-	$\chi^2_1=3.04$	P=0.081
Tameness	-	$\chi^2_1=0.05$	P=0.823
Time	-	$\chi^2_2=3.2$	P=0.202
Region.Age	-	$\chi^2_2=0.92$	P=0.631
Region.Time	-	$\chi^2_3=1.65$	P=0.648
Region.Sex	-	$\chi^2_1=1.19$	P=0.275

[1] Proportion of time spent lying prone could not be converted to normal by taking logarithms (K-S: Z=2.95, p<0.001) therefore a generalised linear model was used on un-transformed results, specifying binomial errors and a logit link function.

Variation in behaviour is not significantly explained by region in any of the cases tested. Time spent relaxing varied significantly with age, with older animals spending significantly less time lying or washing, with most lying occurring in the early morning and evening, but no significant differences were seen between animals inside and outside the park (Figure 44). Similarly, time spent moving was significantly explained by tameness, with animals with higher tameness scores (shyer animals) spending more time moving than tame animals, and an interaction between region and age, with younger animals in Ngorongoro more likely to be moving than elsewhere (Figure 44) but there was no difference in region when controlling for these effects (

Table 52). Animals inside the park were also no more likely to lie prone, with no factors significantly explaining any of the variation between individuals. Finally, four other measures of behaviour were compared inside and outside the park. Data were insufficient to allow rigorous multivariate statistical analysis, but using non-parametric comparisons showed that neither belly sizes, the frequency of hunts or kills were significantly different outside the park. The only behavioural characteristic that did vary was the index of tameness, with cheetahs outside the park significantly shyer than individuals inside (see Table 54).

Table 54 – Comparison of other cheetah behavioural variables using Mann-Whitney U-tests to compare averages

	Outside park		Inside park		Statistic	Significance
	Mean	Median	Mean	Median		
Belly score	2.74 (±0.30)	2.5	2.51 (±0.16)	2	-0.586	P=0.558
Tameness score	1.27 (±0.18)	1	0.25 (±0.08)	0	-6.057	P<0.001
Hunts / hr	0.51 (±0.17)	0	0.96 (±0.24)	0	-0.794	P=0.427
Kills / hr	0.13 (±0.07)	0	0.15 (±0.04)	0	-0.424	P=0.672

Responses to human stimuli

Effect of cowbells on behaviour

Cheetahs

Table 55 – Effect of cowbell playbacks on transformed measures of cheetah behaviour. Playbacks are divided into those played to cheetahs inside the park (subdivided by likely cheetah experience), those played to cheetahs outside the park and controls.

Activity	Before	1st 30 minutes after playback				2nd 30 minutes after playback			
	Mean	Mean	t-test	Prob.	Sig.	Mean	t-test	Prob.	Sig.
Vigilant									
Inside park – no experience	0.81	0.42	$T_7=2.4$	P=0.047	$P<0.05$	0.77	$T_6=-0.62$	P=0.559	NS
Inside park – possible experience	0.97	0.73	$T_{11}=1.53$	P=0.156	NS	0.65	$T_{11}=1.40$	P=0.190	NS
Outside park	0.67	0.45	$T_6=1.25$	P=0.257	NS	0.72	$T_4=0.17$	P=0.874	NS
Control	Insufficient data								
Looking									
Inside park – no experience	0.06	0.39	$T_{10}=-3.86$	P=0.030	$P<0.05$	0.05	$T_9=0.310$	P=0.763	NS
Inside park – possible experience	0.28	0.45	$T_{12}=-2.84$	P=0.015	$P<0.05$	0.11	$T_{12}=2.90$	P=0.013	$P<0.05$
Outside park	0.28	0.48	$T_7=-1.87$	P=0.103	NS	0.20	$T_5=1.65$	P=0.160	NS
Control	0.19	0.38	$T_1=-1.27$	P=0.425	NS	0	$T_1=1$	P=0.500	NS
Moving									
Inside park – no experience	0.15	0.15	$T_{10}=-2.83$	P=0.783	NS	0.21	$T_9=-1.41$	P=0.191	NS
Inside park – possible experience	0	0.14	$T_{13}=-2.61$	P=0.021	$P<0.05$	0.22	$T_{13}=-3.46$	P=0.004	$P<0.01$
Outside park	0.03	0.35	$T_7=-4.36$	P=0.003	$P<0.01$	0.14	$T_5=-1.33$	P=0.242	NS
Control	0	0	$T_1=0$	P=1	NS	0	$T_1=0$	P=1	NS

Transformed responses to playbacks were not significantly different from a normal distribution for either the proportion of time spent vigilant (K-S: Z=0.60, *NS*), looking at the speaker (K-S: Z=0.55, *NS*) or moving (K-S: Z=1.17, *NS*) therefore mean values were compared using paired T-tests (Table 55). The results show that the proportion of time spent looking at the speaker increased for every category of cheetah in the first 30 minutes after the playback, indicating that all subjects could at least hear the recording. This increase was significant for cheetahs tested inside the park but not for those outside or cheetahs played the control tape. Cheetahs outside the park and those inside with probable experience outside the park were also significantly more likely to move in the first half hour following a cowbell playback. However, measures of general vigilance levels did not increase significantly for any categories tested. None of the reactions appeared to last until the second 30 minutes, with the exception of Serengeti cheetahs with experience outside the park, which were still more likely to be moving.

Lions

Only data on the proportion of time lions spent vigilant were successfully transformed to a normal distribution and compared using paired T-tests. Non-parametric tests were used to compare the proportions of time spent looking at the speaker or moving (Table 56). The results showed that, as with cheetahs, the proportion of time spent looking at the speaker increased after the cowbell and control playbacks, especially outside the park. However, the differences were not significant in any region. Nevertheless, it was clear that every lion tested could hear the recording, with all playbacks showing an immediate response in the minutes after the recording. However, differences in the proportion of time spent vigilant were significant for subjects outside the park where lions spent more time sitting up following a playback. Differences in the proportion of time spent moving were not significant, with most subjects not moving at all, giving median values of 0 for each region. However, these results do obscure the fact that some subjects did exhibit a strong response to the playback, both outside and inside the park, and moved rapidly after hearing cowbells.

Table 56 – Changes in proportion of time lions spent vigilant, looking at the speaker or moving before and after cowbell and control playbacks.

Activity	Before playback	30 minutes after playback	Test statistic	Prob.	Sig.
	Mean / median	Mean / median			
Vigilant[e]					
Inside park	0.69	0.66	T_7= 0.282	0.786	*NS*
Outside park	0.61	1.00	T_9= -2.72	0.024	P<0.05
Control	0.61	0.79	T_3= -1.32	0.280	*NS*
Looking[b]					
Inside park	0	0.05	Z=-9.83	0.326	*NS*
Outside park	0	0.2	Z=-2.67	0.080	*NS*
Control	0	0.05	Z=-5.35	0.593	*NS*
Moving[b]					
Inside park	0	0	Z=-1.10	0.285	*NS*
Outside park	0	0	Z=-1.83	0.068	*NS*
Control	0	0	Z=-1.00	0.317	*NS*

[a] Data were arcsine transformed to approximately normal (*Z=0.873*, *NS*; Kolmogorov-Smirnov test) and means were compared using paired T-tests.

[b] Data could not be transformed to normal distribution. Medians were compared using Wilcoxon matched pairs test

Factors affecting responses to playbacks

Cheetahs

Table 57 - Factors affecting three measures of cheetah responses to playbacks. Data were all transformed to a normal distribution and analysed using multiple regression.

		Coefficient	Statistic	Significance
Proportion of time spent looking at speaker				
Playback type		-	$F_{6,31}=1.22$	P=0.321
Wind speed		-	$F_{4,33}=2.49$	P=0.098
Wind direction	Cross	0	$F_{0,37}=3.5$	P=0.041
	Away from cheetah	0.290		
	Towards cheetah	0.474		
Speaker		-	$F_{3,34}=0.03$	P=0.857
Track		-	$F_{5,32}=1.36$	P=0.274
Proportion of time spent vigilant				
Playback type		-	$F_{4,33}=1.16$	P=0.345
Wind speed		-	$F_{2,35}=2.41$	P=0.145
Wind direction		-	$F_{2,35}=1.22$	P=0.309
Speaker		-	$F_{1,36}=0.36$	P=0.583
Track		-	$F_{0,37}=2.6$	P=0.066
Proportion of time spent moving				
Playback type	Inside park	0	$F_{4,33}=2.94$	P=0.035
	Inside park, experienced	0.042		
	Loliondo	0.209		
	Ngorongoro	0.282		
	Control	-0.093		
Wind speed		-	$F_{2,35}=0.31$	P=0.736
Wind direction		-	$F_{2,35}=0.16$	P=0.853
Speaker		-	$F_{1,36}=3.91$	P=0.056
Track		-	$F_{3,34}=1.35$	P=0.275

Table 58 - Factors affecting distance moved and time to first movement of lions following playbacks. Data were normalised by taking natural logarithms and analysis carried out using multiple regression.

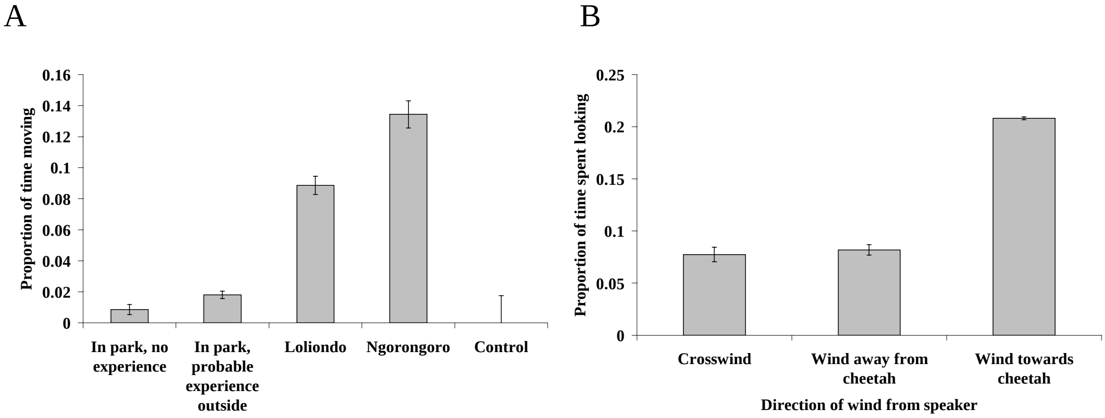
	Coefficient	Statistic	Significance
Maximum distance to the speaker within one hour of playback			
Playback type	-	$F_{4,32}$=1.3	P=0.292
Wind speed	-	$F_{2,34}$=0.67	P=0.518
Wind direction	-	$F_{2,34}$=0.71	P=0.499
Speaker	-	$F_{1,35}$=3.23	P=0.081
Track	-	$F_{3,33}$=0.99	P=0.444
Time to first movement			
Playback type	-	$F_{4,33}$=1.41	P=0.252
Wind speed	-	$F_{2,35}$=0.26	P=0.773
Wind direction	-	$F_{2,35}$=0.43	P=0.659
Speaker	-	$F_{1,36}$=0.95	P=0.335
Track	-	$F_{3,34}$=1.93	P=0.143

Only two factors were shown to explain a significant proportion of variation in responses to playbacks (Table 57 and Table 58). The type of playback was shown to have significant influence on the time spent moving following a playback, with individuals outside the park spending more time moving after hearing a playback than those inside the park and those in the park with likely experience of Maasai spending more time moving than non-experienced animals (

Figure 45 A). Furthermore, wind direction was shown to be an important factor for the proportion of time spent looking at the speaker, with more time spent looking when the wind was towards the cheetah (

Figure 45 B). However, no factors significantly explained the proportion of time spent vigilant (Table 57), or the differences in distance moved and time before the first movement (
Table 58).

Figure 45 – Effect of region / experience on the proportion of time spent moving following a playback (A) and the effect of wind on the proportion of time spent looking at the speaker (B)



Lions

Table 59 – Factors affecting three measures of lion responses to playbacks. Data were analysed using a generalised linear model with binomial errors and a logit link function.

	Coefficient	Statistic	Significance
Proportion of time looking at the speaker			
Playback type	-	$\chi 2_3$= 1.157	P=0.763
Speaker	-	χ^2_1= 0.906	P=0.341
Wind direction	-	χ^2_1=0.414	P=0.520
Wind speed	-	χ^2_2=0.525	P=0.769
Proportion of time spent vigilant			
Playback type	-	$\chi 2_3$= 1.830	P=0.608
Speaker	-	χ^2_1= 0.586	P=0.444
Wind direction	-	χ^2_1=0.02	P=0.888
Wind speed	-	χ^2_2=0.779	P=0.677
Proportion of time spent moving			
Playback type	-	$\chi 2_3$= 0.329	P=0.954
Speaker	-	χ^2_1= 1.075	P=0.300
Wind direction	-	χ^2_1=0.048	P=0.827
Wind speed	-	χ^2_2=0.076	P=0.963

Table 60 – Factors affecting distance moved and time to first movement of lions following playbacks. Data were normalised by taking natural logarithms and analysis carried out using multiple regression.

	Coefficient	Statistic	Significance
Maximum distance to the speaker within one hour of playback			
Playback type	-	$F_{3,17}=1.06$	P=0.393
Speaker	-	$F_{1,19}=0.25$	P=0.626
Wind direction	-	$F_{2,18}=2.06$	P=0.157
Wind speed	-	$F_{1,19}=0.50$	P=0.486
Time to first movement			
Playback type	-	$F_{3,17}=1.06$	P=0.393
Speaker	-	$F_{1,20}=0.00$	P=0.984
Wind direction	-	$F_{1,20}=1.20$	P=0.287
Wind speed	-	$F_{2,19}=0.53$	P=0.595

The proportion of time lions spent either looking at the speaker, vigilant or moving following playbacks could not be transformed to a normal distribution. Therefore analysis was carried out on actual proportions using a generalised linear model specifying binomial errors. Data were available on sex, age and other variables but sample sizes were insufficient to allow their addition into the model. Although control playbacks triggered little response in lions whilst cowbell playbacks caused lions outside the park to spend more time both vigilant and looking at the speaker, sample sizes were too small and standard errors too large for any significant differences to be shown in the analysis (Table 59). Similar problems occurred with analysis of distances moved and the time spent before moving. Data were transformed using natural logarithms, and accepted at the p>0.1 level (K-S: distance moved; Z=1.74, p=0.05, latency; Z=1.76, p=0.04) and regressed against the same potential explanatory factors. Again, movement tended to be quickest outside the park (although the greatest distances moved were inside the park) but differences were not significant (

Table 60).

6.5 Discussion

Diurnal activity

The original hypothesis stated that the larger carnivores outside the park would be less diurnal than inside, to avoid conflict with humans, and that cheetahs might benefit from this. The results of activity of sightings at different times throughout the day confirmed that none of the large carnivore species is strictly nocturnal in National Park conditions, although activity tended to be lowest during the middle, hottest part of the day and highest and the start and end of the day. They also showed that hyaenas and cheetahs were still diurnal to some degree outside the park. Lion activity was not witnessed during the middle of the day outside the park, but low sample sizes restricted the ability to conclude that lions are not diurnal outside the park.

There was some evidence that the degree of diurnal activity was reduced outside the park for hyaenas and lions, with both showing lower activity during the day outside the park, but sample sizes were low and differences were not significant. However, cheetahs showed some evidence to the contrary, with a bimodal activity pattern and the highest activity periods in the mid morning / afternoon. This was demonstrated both in the Park, where such diurnal behaviour is likely to be driven by the activity of the larger, competing predators at night (Caro 1994), but shown to even higher degrees in Loliondo, despite the presence of people during the day. Again, sample sizes limit firm conclusions, but this may indicate that cheetahs are benefiting from the reduced level of diurnal activity of their predators and competitors enforced by human presence and increase their activity during the day where humans are comparably a lower threat. The mechanisms through which similar organisms can coexist with one another on similar resources (see Ebenhoh, 1994 for a general description) have been explored for a variety of taxa (although primarily rodent communities), and important factors identified include variation in body size, foraging efficiency, predation risk, ranging patterns or dietary shifts *e.g.* (Brown *et al*. 1994), (Kotler *et al*. 1994) (Luo & Fox 1996), (Scott 2000). The importance of temporal shifts in behaviour have been suggested as mechanisms for coexistence in some systems, either at a seasonal level *e.g.* (Luo & Fox 1996), (Guerra & Vickery 1998), (Schmidt *et al*. 2000), or some species have been shown to shift daily activity patterns in order to coexist *e.g. Drosophila sp.* parasitoids (Fleury *et al*. 2000) or desert gerbils (Kotler *et al*. 1993). If the daily activity of cheetahs is strongly determined by lions and hyaenas, as suspected (Caro 1994) and as would be expected following the demonstrations of avoidance behaviour at a local level (Durant 2000a), then the presence of humans in the environment could be benefiting the cheetah simply by enforcing this temporal separation. However, much more work is required here to demonstrate the effects, if any, of losses of cheetah kills and cub mortality in the buffer zones before this theory can be demonstrated more clearly.

One surprising result common to all three species was the low activity levels before 07:00 recorded in Loliondo and Ngorongoro for hyaenas, a result that directly contradicts the expectation that activity would be highest furthest from the middle of the day. Although such a result might be expected for cheetahs if they were avoiding periods of high lion and hyaena activity, the fact that activity of all three predators is low at this time suggests a common cause. This may be the low sample sizes obtained for this restricted time in the morning (light was not sufficient for many sightings before 06:00 and work rarely began before this time) causing increased stochasticity in the results. An alternative explanation may be that this is the period when most Maasai start to move their cattle from their bomas, causing carnivores to lie low for this period of high human activity.

Focal-followed cheetah behaviour

The most striking result of the detailed observations of cheetah behaviour was the homogeneity of activity budgets between the three areas. Activity, measured as time spent relaxing, moving or lying prone, varied to some degree with the age of the animal, with younger animals generally more relaxed and less active (with the exception of Ngorongoro where the reverse was true, although this result was skewed by a single female who was active for almost the entire time she was observed). Activity levels varied across the day, but no overall differences between the three regions were observed and examination of the pie chart results shows that proportions were almost identical. Such results are surprising if living in a buffer zone is more stressful, since when stress has been demonstrated in cheetahs (*e.g.* (Caro *et al*. 1989)) it is associated with changes in behaviour and increased time spent alert. Furthermore, initial exploration of hunting behaviour, kill success and belly size measurements revealed no differences between individuals inside and outside the park. These results are unlikely to be due to any experimental error since sample sizes were large, standard errors were low, behaviour types could be easily classified and measurement was carried out to the nearest second.

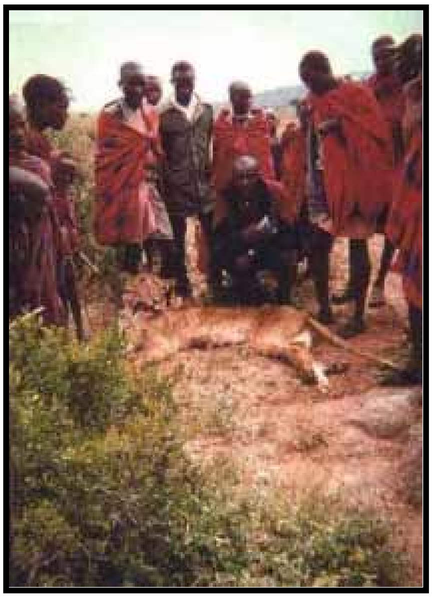
Levels of relaxed behaviour or activity are likely to be determined by either prey or threats (perceived or actual) (Caro 1987). The lack of difference in belly sizes and hunt success support the results of chapter three that suggest access to prey outside the park is unlikely to differ from that inside the park for large carnivores. The main threats to cheetahs inside the park are from lions and to a lesser extent from spotted hyaenas, through loss of kills and direct predation (Caro 1994). Outside the park it was expected that humans would comprise a significant, additional perceived or actual threat. Chapter four showed that levels of lions outside the park were not significantly different from areas surveyed inside the park and that substantial populations of hyaenas also existed. It might therefore be expected that the influence of larger predators on cheetah behaviour were equivalent both inside and outside the park and that humans would constitute the main difference. The fact that no significant differences were observed shows that the mere presence of humans in the environment does not cause a shift in cheetah activity budgets and does not cause stress to the extent that cheetahs would naturally suffer under other circumstances (*e.g.* non-territorial males - Caro *et al*., 1989)

Effect of human stimuli

The results of the playback experiments suggest that reactions to human stimuli do occur, but there was no single behaviour type that could be attributed to animals outside the park, as was expected. Playbacks were heard, as demonstrated by the increase in looking by all categories, and were distinguished from control playbacks by animals expected to recognise the difference, but levels of reaction to playbacks were mixed, with lions outside the park looking at the speaker more and cheetahs outside the park or with experience moving more. However, differences between inside and outside the park were insignificant for most measures of response (including distance moved, showing that the differences in proportion of time spent moving were not necessarily showing cheetahs moving away from the speaker but merely shifting their positions). The only other significant variable was shown to be wind direction, with more time spent looking at the speaker when the wind was towards the cheetah, presumably because the sound was clearer or louder. One of the main reasons for the lack of significant results is possibly the variability of responses. Although several cheetah and lion subjects reacted very strongly to cowbells outside the park, moving rapidly after the start of the tape and settling down again a long distance from the speaker, other individuals showed no apparent reaction beyond an initial increase in time spent looking at the speaker. In one cheetah and one lion example, the individuals were within a few hundred metres of Maasai villages at the time therefore the chance that they had not experienced humans was remote. Furthermore, one lion sighting consisting of three very young and thin individuals in Ngorongoro, moved towards the speaker. Although these data are insufficient to draw any conclusions, it is interesting to note that the only lion attack for which photographic evidence was obtained during the study involved a similarly young and poor condition individual (Figure 46). Equally, most individuals inside the park showed little reaction to cowbells beyond the slight differences shown by cheetahs with probable experience outside. However, occasionally both lions and cheetahs inside the park responded very strongly, moving a large distance very quickly. Since the sample sizes were fairly limited for each category, such results had major effects on the overall results. Unfortunately, very little work has been carried out on responses to humans, although it has been demonstrated that certain species in human environments can become very sensitive to the threats imposed by humans, *e.g.* (Bshary 2001). Of the literature available, most refers to flight distances of ungulates (*e.g.* (Aastrup 2000) (Borkowski 2001), (Colman *et al.* 2001), (Martinetto & Cugnasse 2001) or responses to habitat disturbance (Linnell & Andersen 1995)). Of these, there are mentions of rapid habituation to humans, even under hunted conditions, which is a possible explanation for the split in behavioural patterns witnessed here. Alternatively, some models investigating the optimal strategies for vigilance show that vigilance behaviour is strongly affected by the chances of predation and the effectiveness of vigilance (Brown 1999) . Since the study areas are open, it is unlikely that the effectiveness of vigilance is poor. Therefore the lack of vigilance by some individuals merely indicated a lack of experience of humans as a threat. However, in many of the game models, vigilance is assumed to compete with foraging as a behaviour type (Ward *et al.* 2000), (Dall *et al.* 2001). Since large carnivores spend a large quantity of their time resting and not looking for food

(Schaller 1972b), (Caro 1994) and do not need to stop feeding to be vigilant, the costs of vigilance would be much lower. An alternative theory might be that two strategies for avoiding humans are employed by carnivores outside the park. In many cases, the strategy is to move away as quickly as possible. In other cases, individuals seemed to prefer to lie low, possibly to avoid attracting any attention to themselves.

Figure 46 - Maasai and a young lion that was killed inside their boma, near Wasso, Loliondo Game Controlled Area. Photo credit: Laura de Luca



Limitations of the study

The primary limitation of the investigation into daytime activity was a lack of data. Although overall sample sizes of sightings were good, the number of sightings at certain periods of the day outside the park were low. From time spent in the field, it was strongly suspected that lions and hyaenas were less active in the day, since they were noticeably absent, despite equivalent or near equivalent population sizes to those in the park, but this was not shown satisfactorily by the data available. The dataset was also limited by the assumption of randomness. Although sightings that were seen to move as a response to the car were recorded as not moving, it is quite likely that a large number of sightings were missed because they were not active and that this dataset represented an overestimate of the number of active animals in all areas. Possible solutions include reanalysis using different time periods to group data, although this would lose the subtleties the analysis is trying to show. Alternatively, carnivore behaviour should be collected intensively on a number of individuals inside and outside the park using methods similar to the cheetah focals to avoid the assumption that sightings whilst driving are truly random.

Behavioural focals were limited by two primary factors. Firstly, the assumption that chosen categories of behaviour were accurate may not be true. For example, differences between vigilance behaviour due to predation risk and hunger are notoriously hard to distinguish (Caro 1987), whilst some work even suggests that apparently non-vigilant individuals are still being vigilant to a certain level (Lima & Bednekoff 1999) and there is a risk of classifying behaviour according to known human behavioural patterns rather than categories more appropriate for cheetahs. Secondly, despite the large time spent following individuals, the dataset was still limited in terms of representation by certain categories of cheetah. For example, with more data it would have been possible to control for group size, which is known to affect vigilance (Fitzgibbon 1989), (Clutton-Brock *et al*. 1999), (Robinette & Ha 2001) or litter size and age of cubs (rather than presence / absence) (Caro 1987).

Analysis of responses to playbacks was confused by the lack of a distinct response to cowbells, with some individuals responding extremely strongly and others not at all. It is possible that responses were determined by factors not included in this analysis, for example the age, sex and number of cubs present, distance to nearest human habitation or distance to park boundary, but insufficient data were collected to model variation of all these factors. The only solution to this would be to increase sample sizes with more playbacks. Larger sample sizes would also have been preferable for the control playbacks, with addition of different control noises to eliminate any possibility any reactions were due to the control chosen. However, it might also be worth running the analysis again using different cut-off points to compare behaviour, for example comparing pre-playback behaviour with the first minute, five minutes and ten minutes after the tape is started to try and determine differences in more subtle changes of behaviour such as looking at the speaker or initial periods spent scanning the surroundings.

Chapter 7: The role of Maasai in carnivore ecology

7.1 Summary

In this section, the role of Maasai in carnivore ecology is investigated and potential mechanisms allowing coexistence are discussed. Using 179 interviews of male respondents in Loliondo and Ngorongoro, attitudes towards carnivores and the levels of conflicts experienced are assessed. The results show that lions, hyaenas and leopards are major components of the Maasai perception of wildlife with all recording high salience scores. Attitudes are generally negative, with all large carnivores classed as problem species, although over half of respondents in Loliondo were positive towards wildlife in general. Respondents in Ngorongoro tended to be more negative than Loliondo with only 38% thinking wildlife was a good thing in general and 77% thinking someone should control wildlife levels. However, recognition of the cheetah was surprisingly poor in all areas, with low salience scores and approximately half of respondents unable to differentiate them from leopards. Costs of coexistence were high for both Maasai and carnivores. 89% of respondents in Loliondo and 63% of respondents in Ngorongoro reported at least one attack on their livestock by a predator, with losses accounting for an average of 0.96 ± 0.26% of cattle herds and 3.06 ± 0.62% of shoat herds, although the major source of livestock loss was disease which accounted for approximately 30% of losses. There was no difference in the proportions of attacks carried out by different carnivores in either area (χ^2_4=1.61, *NS*) with lions, leopards and hyaenas responsible for most attacks. Attacks on people were comparatively rare, with lions were the main species responsible, but 30% of Loliondo bomas reported an attack on a member at some point. However, 71% of these attacks in Loliondo and 50% in Ngorongoro occurred when the victim was hunting lions. Reports of indirect persecution were relatively low, with only 40% of Loliondo respondents and 25% of Ngorongoro respondents claiming to have ever used poison or snares and almost all (75% Loliondo, 100% Ngorongoro) in response to attack. However, 60% of respondents in both areas reported to have physically killed a predator at some point, with lions, leopards and hyaenas the main targets respectively. The lion hunt is still a major part of Maasai culture with 85% of Loliondo respondents and 74% of Ngorongoro respondents reporting having participated in at least one, removing an estimated 30-40 lions from the entire

Tanzanian and Kenyan Maasailand. However, hunts are limited temporally, spatially and by choice of weapons. It is concluded that the relationship between the Maasai and the large carnivores is far from harmonious for either party; however, Maasai influences are low enough to allow large carnivores to persist in the area.

7.2 Introduction

Impacts of Maasai on their environment

Historical evidence suggests that in the past the Maasai have had a negligible, or even beneficial, impact on wildlife. For example, mapping current protected areas with the historical boundaries of Maasai distribution shows a strong correlation, with all the areas seen as most valuable for conservation being integral parts of Maasailand (Parkipuny 1997). This probably reflects the attributes of the land that attracted both wildlife and the Maasai, but unlike many other areas that attract people and animals this did not result in the expulsion of one by the other. Indeed, various comments were made by the first explorers to meet the Maasai on the richness of their environment. In 1887 Joseph Thomson described the Maasai as non-hunters of animals, with the resident wildlife showing little fear of people (Collett 1987) and other travellers were overwhelmed by the numbers of animals in the area (Parkipuny 1997).

One of the most debated relationships between Maasai and their environment is that of the impact of Maasai cattle on wildlife. Evidence for a detrimental effect has come from the Loliondo region of Tanzania where it has been argued that overall biomass is equivalent to the neighbouring Serengeti, but that cattle replace wildebeest as the dominant herbivore (Watson 1969), whilst in Nairobi National Park the removal of cattle led to a 5% rise in wildebeest numbers (Watson 1969). With the help of man, cattle could potentially out-compete wildlife. However, various management techniques employed by the Maasai, together with the restrictions placed upon them, mean their impact is usually far lower than is often assumed (Homewood & Rodgers 1991). The well-studied Maasai of the Ngorongoro region appear to have had little detrimental effect on their environment (Arhem 1985), (Homewood & Rodgers 1991), with little competition between wildlife and cattle due to the exploitation of different resources and compatible movement cycles (Machange 1997), although competition increases to the north (Makacha 1982) and is evident on the short grass plains (Machange 1997). However, there has actually been a rise in wildlife numbers during Maasai presence, with unfavourable disease interactions allowing wildebeest to completely out-compete cattle in some areas (Homewood & Rodgers 1987; Homewood & Rodgers 1991), (Machange 1997). Sometimes Maasai cattle are still blamed for environmental damage even when evidence suggests otherwise. In one study to determine the cause of wildebeest decline in the Serengeti-Mara ecosystem in Kenya agricultural expansion rather than livestock competition was found to be the primary cause. However, it was still suggested that the Maasai should take the blame for this for forcing the wildebeest into competition with agriculture in the first place and by leasing their lands to agricultural farmers (Ottichilo *et al.* 2001). Finally, concerns have also been voiced for the impact of cattle removing nutrients from one area and depositing them near the pastoralist settlement. This could cause particular problems at certain times of the year for wildlife, such as lactating wildebeest that require calcium-rich grasslands, whilst trampling by the large cattle herds is said to damage the environment. However, when investigated, little evidence was found to support the nutrient loss theory whilst the migration of wild animals is thought to cause more damage than cattle trampling (Homewood & Rodgers 1991).

The Maasai and hunting

Traditionally, Maasai hunt no ungulates other than buffalo and eland and there is a distaste towards those that eat wild meat (Spencer 1988), (Homewood & Rodgers 1991). There are reports that these traditions are not rigorously upheld at all times, for example poaching for trophies has been recorded occasionally *e.g.* (Makacha 1982) and conflict can occur between age sets when occasionally the younger generation will do exactly the opposite to the wishes of older generations, which can lead to hunting (Homewood 1995). Ironically, some of the best examples of Maasai hunting of wildlife have occurred since the introduction of conservation strategies designed to protect wildlife but at the expense of pastoralist residents. For example, antagonism between park management and Maasai resulted in rhino killings in Amboseli, Kenya (Collett 1987) and in the Ngorongoro Conservation Area (Homewood & Rodgers 1991). However, the impact of hunting by the Maasai on, for example, the Serengeti ecosystem is still thought to be negligible (Campbell & Hofer 1995).

Although hunting is unlikely to have a major effect on ungulates, the impact on carnivores may be more substantial, in particular for lions. Part of Maasai tradition is the lion hunt, or *olamayo*, a privilege of the *murran* (young warrior) that symbolizes their role of defending the cattle that is still practiced relatively frequently (Spencer 1988), (Homewood & Rodgers 1991), (Kipury 1993). Although many *murran* participate in the hunt, only one can claim the prestigious mane, which is awarded to the first *murran* to spear the lion. If the lion is successfully killed, the troupe then returns singing to the bomas, participating in a dance and enjoying the attentions of the young women (Spencer 1988).

Habitat losses

Although predominantly pastoralists, the Maasai use agricultural products to supplement their diet and often trade livestock products for grain (Thompson 1998). Some Maasai around Arusha in Tanzania have even become exclusively cultivators. However, use of small-scale agriculture is increasing amongst the Maasai (Parkipuny 1997) for a variety of reasons including national persuasion, economic incentives and land tenure issues (Thompson 1998). The current impact of small-scale agriculture is minor and contestable (Homewood & Rodgers 1991), but this may change if agriculture becomes more widespread. However, the Maasai cannot be expected to ignore opportunities to raise their standard of living and there will always be pressures driving development to increase income or resources (Norton-Griffiths 1995). One survey of southwest Tanzanian Maasailand has shown nearly 50% land clearance for cultivation over the last thirty years, together with nearly 80% removal of woodlands, changes blamed upon the lack of land-use planning and increase in population (Mwalyosi 1992). Further examples of the effect of conversion to agriculture can be seen at Tarangire National Park in northern Tanzania, which has been increasingly surrounded by lands used for intensive agriculture. These have restricted migration routes and increased conflict between resident and local herbivores (Borner 1985). Equally, in the Serengeti ecosystem it has been estimated that 30% of the wildebeest population could be lost if the Kenyan Mara buffer zones were cultivated (Norton-Griffiths 1995).

The Maasai and conservation

Theoretically, the Maasai appear to be highly compatible with conservation policies (Parkipuny 1997). This could be attributed to an active respect for their environment (Spencer 1988) or that they are just incapable of over-exploiting the environment further with their present lifestyle (Norton-Griffiths 1995). Certainly the low emphasis on hunting and agriculture means that even their very presence can be important, since most inhabit and allow the use of vital grazing grounds for wildlife (Collett 1987). However, the Maasai have suffered for a long time under increasing imposition of restrictions in the name of conservation (Collett 1987), (Monbiot 1994). One of the best examples is the case of the Serengeti region in Tanzania. Despite a long history of coexistence between Maasai and wildlife in this region, the Maasai have gradually lost large amounts of land across the past century (Parkipuny 1997). In 1940, the first legislation established the Serengeti, including the Ngorongoro highlands, as a reserve, recognising the rights of the existing Maasai to live there. However, in the 1950s increasing pressure from Europe and North America called for the establishment of full National Park status, removing the people within its borders (Parkipuny 1997), (Shivji & Kapinga 1998). Following protests from the Maasai a compromise was reached in 1958, forming the Ngorongoro Conservation Area (NCA). This gave the Maasai guaranteed rights and compensatory water supplies in return for the establishment of the Serengeti National Park and eviction of the Siringet and Salei Maasai from its borders (Arhem 1985), (Parkipuny 1997). However, since then the rights of the Maasai in the NCA have slowly been eroded, with the failure of the water supplies (Parkipuny 1997), their exclusion from the NCA decision-making body in 1961, the banning of agriculture in 1975 (Thompson 1997), bans on forest resin collecting, restrictions on fire use and their removal from within the crater itself (Arhem 1985). All of these changes were made despite the increase in wildlife, stability of the livestock numbers and lack of evidence for overgrazing or erosion (Homewood & Rodgers 1987). Few conservation policies involve the Maasai, despite their knowledge of arid-rangelands and experience in the area (Arhem 1985) and various calls for multiple use areas (see Introduction, p.240). Although the Ngorongoro environment has been successfully protected, the Maasai economy is in a serious state of decline, with an increasing percentage unable to support themselves through pastoralism and evidence of malnutrition (McCabe *et al*. 1992). Similar experiences with the conservation authorities in other areas such as over property rights in the Mara region (Norton Griffiths 1996) or Amboseli in Kenya (Western 1982), have left many Maasai mistrustful or antagonistic towards any future conservation changes (Parkipuny 1997). In the NCA, conservation policy is seen as legislation that does not consider the Maasai - in 1983 90% of Maasai children thought conservation was for tourism purposes only (Homewood & Rodgers 1991)

Previous studies of attitudes and impacts on communities

Previously, conservation science frequently ignored the attitudes of local people (Hackel 1990), but concurrent with the rise of interest in semi-protected areas has been a realisation of the need to recognise the attitudes and perceptions of people living in and around these areas before conservation plans can be effective *e.g.* (Child 1991), (Heinen 1993), (Campbell & Borner 1995), (Mehta & Kellert 1998), (Uphoff & Langholz 1998), (Hoare 2000) (but see (Low 1996)). Surveys of attitudes towards conservation have since been used to investigate attitudes towards a wide range of conservation targets and issues, including mountain lions (Manfredo *et al*. 1998), Asian lions (Saberwal *et al*. 1994), tigers (Sekhar 1998), crop raiding (Studsrod & Wegge 1995), (De Boer & Baquete 1998), (Sekhar 1998), vegetation conservation (Lykke 2000) or the success of community conservation projects *e.g.* (Gillingham & Lee 1999). Common findings have been to show support for conservation in general, but not for the external institutions responsible *e.g.* (Harcourt *et al*. 1986), (Infield 1988), (Hackel 1990), (Parry & Campbell 1992), (Kangwana 1993), (Akama *et al*. 1995), (Fiallo & Jacobson 1995), (Nepal & Weber 1995a), (Gillingham & Lee 1999). For example, Newmark showed 71% of people opposed to abolishing National Parks whilst 71% also had negative attitudes towards the park employees (Newmark *et al*. 1993). However, positive attitudes are less common in response to questions about carnivores, which frequently revealed very negative attitudes *e.g.* (Kellert *et al*. 1996), (Pate *et al*. 1996), (Breitenmoser 1998).

Factors thought to be driving attitudes are varied. In some cases positive attitudes towards protected areas are primarily driven by utilitarian reasoning, with 41% of respondents stating revenue from tourists as an important benefit of protected areas, although ethical reasons were third with 12% (Newmark *et al*. 1993). Other studies have shown improved access to wildlife-related benefits does not necessarily improve attitudes (Parry & Campbell 1992), (Gillingham & Lee 1999). Social status and sex also appear to be influential, with wealth shown to be positively correlated with tolerance (Infield 1988), (Newmark *et al.* 1993), women less tolerant (Kangwana 1993), (Gillingham 1998) and young adults and educated individuals the most tolerant, although often factors are hard to pull out due to the range of issues (Gillingham 1998). The main cause of negative attitudes appears to be the impact on land use, with Newmark showing 44% citing this as a reason for negative attitudes followed by wildlife conflict with 22% (Newmark *et al*. 1993). The same study also showed that negative attitudes towards parks were greater for groups who had lost land as a result of the park establishment and for those who depended more on wildlife resources. Thus agricultural people near the Selous Game Reserve were less well disposed towards the reserve than pastoralist residents near Arusha, Tarangire and Manyara National Parks (Newmark *et al*. 1993). Elsewhere, negative attitudes towards lions in Gir, Western India, were poor due to a high prevalence of attacks and dissatisfaction with the compensation (Saberwal *et al*. 1994).

Many attempts have also been made to quantify conflict, and the results show levels of predation vary greatly. In a 33 km^2 area bordering the Sengwa Wildlife Research Area, Zimbabwe, 241 livestock were killed in just over 3 years by wild animals, with lions, leopards and baboons the most serious problems. Attacks cost an average of 12% of each household’s income and were most frequent in the dry season (Butler 2000). In Waza National Park in Cameroon 700 cattle and 1000 sheep and goats are reported lost annually around the park due to lions, more than any other carnivore and equalling losses to disease (Bauer *et al*. 2001). Problems appear to be especially high in Nepal, with losses to wolves and snow leopard accounting for an average of 18% of livestock, the equivalent of about half the annual income (Mishra 1997), whilst the lions in Gir were thought to be obtaining 75% of their food from livestock in 1975, falling to 30% in 1995 (Singh & Kamboj 1996). However, such examples of very high losses appear to be in the minority, with some studies admitting vulnerability to exaggeration (Bauer *et al*. 2001). In Kenya, Mizutani found predation was the second highest cause of livestock loss after disease (15-20% and 60% respectively), accounting for 0.8% cattle and 2% sheep per (Mizutani 1993) whilst in Zimbabwe, Rasmussen showed most reports of predation were false and losses to wild dogs were negligible (Rasmussen 1999).

Chapter aims

In this section, the role of Maasai in carnivore ecology is investigated in order to examine their potential role in determining carnivore success. For this, four main questions are examined:

1. What are the Maasai attitudes towards, and perceived conflict with, the carnivores? Do these show potential for a major influence on carnivore ecology and are their impacts likely to differ for cheetahs?
2. What is the *actual* impact of carnivores on Maasai through livestock predation and threat to human life? Do cheetahs have a lower impact than other carnivores?
3. What is the actual impact of the Maasai on the carnivores and who exerts the greatest impact? Are impacts on all carnivore species equivalent?
4. Do the interactions between Maasai and carnivores reveal how any level of coexistence is occurring?

7.3 Methods

Overview of methods

Several methods were employed to investigate the Maasai–carnivore relationship. The primary method was a large scale interview survey used to investigate attitudes towards the carnivores, to assess the level of interactions between the Maasai and carnivores and to investigate future directions. Secondly, re-visit interviews were conducted, visiting respondents repeatedly in an attempt to support quantification of the frequency of conflict incidents, using the previous visit as a reference point for more accurate estimates of time. Thirdly, event diaries were used to cross reference both general and lion hunt interview data and attempt to get a firm understanding of the frequency of events. Fourthly, interviews focussing specifically on the lion hunt were conducted to determine its cultural relevance and the extent of its impact. For a full copy of the questionnaires, please see Appendix VI (p.371).

General questionnaire survey

Sampling strategy

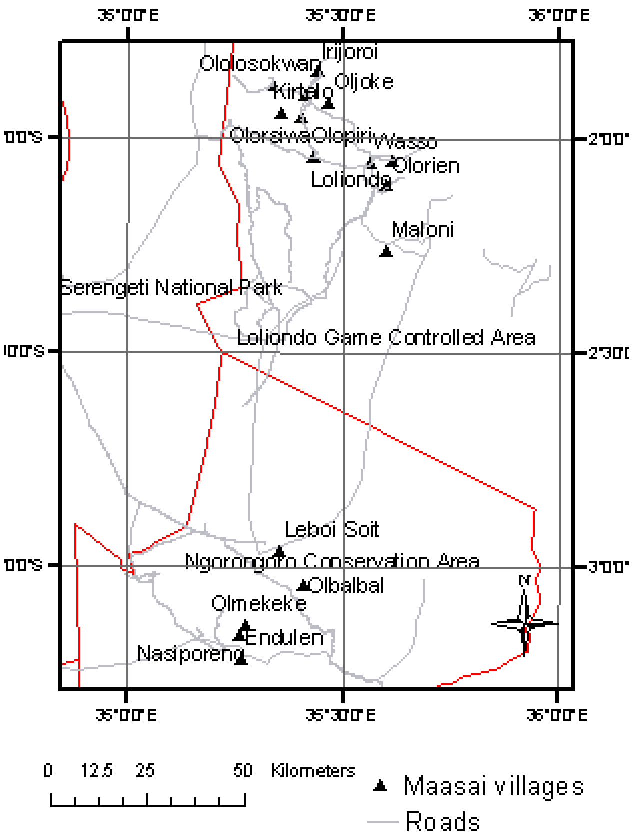
Sample area

The villages surveyed included all of those that used the wildlife study area for grazing, with the exception of Arash where a number of recent car-hijacking incidents deemed it unsafe to visit. The villages focussed upon in Loliondo were Ololosokwan / Mairoa, Olorsiwa, Olopiri and Olorien (see Figure 47). Other villages were visited opportunistically, or to find specific individuals for lion hunt interviews (see “Lion hunt (*olamayo*) interviews”, p.257).

Target interviewees

Interviews were targeted at men only. Ideally, the household head was interviewed, but interviews were also conducted with junior elders if the head was unavailable. Interviews included the village chairman to represent political decision makers (Gillingham & Lee 1999). Restriction to male interviewees was partly for logistical reasons, since etiquette states it is the household heads who need to be approached initially (Kangwana 1993) whilst women and children take a more background role, but it was also assumed that older men, who make all of the major decisions within the community, would be those with most influence over their environment. Furthermore, older men make up a relatively small proportion of the total population less than 15% in the Soit Sambu area (Bureau of Statistics 1988), (Ngorongoro Conservation Area Authority 1999), therefore making it easier to sample a representative proportion. Some interviews were also carried out with *murran*, due to their traditional role in predator hunting and livestock protection.

Figure 47 - Map of the main villages in the study area



Targeted sample size

Determining sample sizes and sampling frames requires information on existing populations. However, published demographic data on nomadic, pastoral populations are generally scarce (Roth, 1986) due to limited resources, the complications of borders that are ignored by nomads and partly to the attitudes that pastoralists are marginal and therefore less important members of the national population (Coast, 1997). Nevertheless, Tanzania has published national censuses roughly every ten years since independence. The most recent published census available to this study stated there to be approximately 6500 people in the villages around the study area, although this is over ten years old (Bureau of Statistics 1988). Despite its obvious flaws, there was little choice but to base the target sample size on the 1988 population figures since they were the only complete data for the region. Since attitudinal surveys tend to require smaller sample sizes (Oppenheim 1992) a target of 10% coverage was chosen (as used by Kangwana, 1993). Assuming adult men to refer to over 18 year olds, the target sample sizes for Loliondo as calculated from the National Census are presented in Table 61. In Ngorongoro, a less rigorous methodology was applied.

Since the population is thought to number approximately 25,000 (Perkin 1995), due to time limitations and data availability there was no opportunity to approach the Ngorongoro study area in the same way. Instead, all of the villages using the study area used for wildlife surveys were identified by informal questioning and the maximum number of interviews possible carried out in the remaining time. It is therefore acknowledged that the results may be more open to bias than a truly randomly sampled population.

Table 61 - 1988 National Census data for Soit Sambu ward and targeted sample sizes

Village	Data	Female	Male	Grand Total	Target sample size to sample 10% adult men
Ololosokwan	Children	427	389	816	0
	Young adults	224	109	333	0
	Adults	282	220	502	23
Olopiri	Children	166	226	392	0
	Young adults	95	40	135	0
	Adults	86	103	189	11
Soit Sambu / (Olorien?) [1]	Children	391	372	763	0
	Young adults	111	132	243	0
	Adults	300	275	575	28
Soit Sambu	Children	660	714	1374	0
(Including sub-villages)	Young adults	237	228	465	0
	Adults	520	381	901	38
Total number of people		3499	3189	6688	100
Total number of children		1644	1701	3345	0
Total number of young adults		667	509	1176	0
Total number of adults		1188	979	2167	100

[1] **Soit Sambu is mentioned twice in the census, presumably due to a publishing error. It is assumed that the smaller value refers to the slightly smaller village of Olorien / Magaduru, which is missing from the census**

Sampling frame

The chosen sample unit was the household or *olmarei* as these were the basic unit of shared economic production, although some questions were based at the boma level. These are marked later in the methods. Ideally the interviewed sample should be randomly drawn from the population (Oppenheim 1992), however, as has been found with previous surveys of the Maasai (Coast, E. *pers. comm.*), (Thompson 1998) and other areas in Tanzania (Newmark *et al*. 1993), the sampling frame provided by the National Census is inadequate for rigorous scientific sampling. Instead, a less formal sampling method was used. When a village is first entered, a village official (chairman or secretary) was asked to help draw a sketch map of the area showing the location and names of bomas, numbers of gates (households) in each and other land features. From this, bomas were numbered and drawn randomly for interviewing. Within each chosen boma, the aim was to interview at least two respondents to allow verification of boma-based questions.

Interviewers

Interviews were carried out by myself, using a resident Maa-speaking guide from Loliondo (Jacob Ole Koriata, Ilbaluka age set) and Ngorongoro (Kaleya Ole Tall, Ilkishili age set) for translation, or by the translators on their own after careful training. Both translators spoke Maa as their first language, were resident in their respective areas and most of the respondents and spoke near-fluent English.

Introductory, social and economic questions

Before starting a questionnaire introductions were made, disassociating the project from local authorities and NGOs and explaining its purpose, but without specifying an interest in carnivores. The respondent was then asked basic questions on his age and *olmarei* to determine his social and economic status (Table 62, Table 63).

Table 62 – Data collected on respondent status

Data	Notes
Base information	Village, date, respondent name, interviewer name
Others present	Ideally interviews were conducted privately to avoid influence of non-respondents, but this occasionally caused suspicion in which case others were permitted to be present
Age	Both age in years if known and age set name. All respondents knew their age set.
Olmarei size	Total number of men, women and children within the respondent's *olmarei*.
Livestock	No. of cattle, shots (sheep and goats) and donkeys owned by the respondent.
Crop status	Does the respondent grow any crops (Y/N)

Table 63 – Data collected on livestock dynamics

Data	Notes
Livestock gained over the past month	Number of cattle / shots gained through births, purchase, gifts or other means
Livestock lost over the past month	Number of cattle / shots lost through natural deaths (disease etc.), slaughter, sale, gifts, stolen, predators or other means
Livestock guards	Details of those normally given responsibility over livestock
No. dogs	Number of dogs in whole boma

Perceptions of wildlife and variation in attitudes

Using attitude scaling

One of the most important interactions between the people and wildlife of the buffer zones is the perceptions of one another, since even if a predator is not a realistic threat to livelihood, but is perceived as one, persecution will still occur (*e.g.* see (Cowlishaw 1997), (Villafuerte & Moreno 1997), (Cowlishaw 1998), (Gosler 2001) for discussion of the effect of perceived threat on behaviour). Furthermore, variation between perceptions of different carnivore species is important if lesser predators such as cheetah are to gain by Maasai persecution of other predators, since if risk perceptions for personal or livestock safety vary between species then it is likely that those perceived as more unfavourable will be persecuted more. Thus, if lions and/or hyaenas are seen as less desirable they may be hunted or discouraged to the cheetahs benefit. However, attitude surveys are extremely hard to carry out, since the answers can depend heavily on questionnaire wording, the respondent’s desire to express true feelings or even not knowing their true feelings (Oppenheim 1992). Furthermore, attitudes are almost impossible to validate since there is no reliable source of external information for cross referencing (Oppenheim 1992). Several tests of attitudes are therefore employed in this study.

Free-listing

Firstly, attitudes were assessed using free-listing; asking the respondent for all of the wild animals they can think of that live in the area and assuming that the frequency and order that different species were mentioned was an indication of perceptions. Free listing also provided a good introduction to the interview, allowing the respondent and interviewer to chat generally about wildlife, creating a positive atmosphere for further questioning. As much time as required was given and up to thirteen animals recorded, in the order they were mentioned. From the free lists, two categories of information were extracted:

1. The importance of carnivores as a grouping: It might be an assumption to think that the biological classification of carnivores was a valid grouping for the Maasai. The first section therefore aimed to place the carnivores within the general perception of wildlife, to see if they are perceived as a distinct entity and to judge their importance when discussing wildlife. The existence of a perception of carnivores as a distinct group was tested by analysing which species were mentioned together in the lists and then compiling a matrix of average "distances" between all possible species pairings (for example, the species mentioned 3rd and 4th had a distance of 1, species mentioned 3rd and 7th had a distance of 4). Using the average distances as a measure of association between each species, multi-dimensional scaling (MDS) was then carried out to represent the associations graphically on a scatter plot allowing identification of approximate groupings (Bernard 2002). All analysis was carried out using Anthropac (Borgatti 1990).
2. The salience of carnivores in relation to other wildlife: Respondents were assumed to mention the most salient items more frequently and earlier in the list (Bernard 2002). The general importance of carnivores with respect to other species was therefore investigated by looking at the relative frequency of mentions and by an index of salience (S) measured using an index of 0-1 representing the relative position on each list (S_j) and the number of times each animal was mentioned (adapted from J. Jerome Smith's formula quoted in documentation accompanying (Borgatti 1990)):

   $$S = \frac{\sum S_j}{N} \text{ Where } S_j = 1 - \frac{r_j - 1}{n - 1}$$

   S = saliency index value
   N = Number of free lists
   r_j = Position of item j in list
   n = Number of items in list

Picture cards

Picture cards were also used to investigate two aspects of attitudes towards wildlife and the carnivores. Firstly, the status of carnivores as problems with respect to other species was investigated by presenting a range of photographs of seventeen wild animals (lion, hyaena, leopard, cheetah, wild dog, jackal, serval, crocodile, giraffe, Thomson’s gazelle, wildebeest, zebra, buffalo, elephant, rhino, hippo, snake) and asking respondents to place them into three piles representing those they considered no problem to them, those they considered a small problem and those they considered a large problem. The species chosen represented the most important to the Maasai as represented by at least 50% of respondents in free lists as well as examples of rarer species that may represent a problem if present such as the crocodile and rhinoceros. A picture of a serval was also added, although never mentioned in free lists, in an attempt to clarify ability to distinguish between the spotted cats. Analysis was carried out using a variation of attitudinal scaling (Oppenheim 1992), placing each species on an arbitrary scale representing their perceived problem status. Using the piles determined by the respondent, each species was given a score of “1” if classed as a big problem, “2” if classed as a small problem and “3” if not seen as a problem at all. Mean scores were then calculated for each region.

Secondly, having determined the immediate placing of carnivores with respect to other wildlife, differentiation between individual species was tested. Picture cards were used to reintroduce the four large carnivore species thought to be most important in the area, namely lions, hyaenas, cheetahs and leopards. Again, photographs were used, chosen to represent the species as accurately as possible to reduce confusion due picture recognition. For example, cheetahs were represented by a pair of adults, the leopard by a close up of a single adult in a tree and hyaenas as part of a group feeding on a carcass. In addition, a picture of a wild dog was included as a control with the idea that it would identify respondents who were making up answers (Oppenheim 1992), (Bernard 2002), since wild dogs were thought to be extinct in the Serengeti (Woodroffe *et al*. 1997) but not too unusual a choice to raise suspicion. The local, Maa word for each species was then asked for and recorded to check simple ability to differentiate. A quick description was then asked for, recording the first three points mentioned to give an immediate impression of attitudes towards each species. Answers were recorded in longhand and then coded into the predominant categories.

Attitudinal questions

Finally, general attitudes towards the environment were assessed with three basic questions. Firstly, respondents were asked what they thought about having wild animals around their village. Secondly, they were asked if they would like somebody to control the numbers of animals that lived around them. Finally, their thoughts on either the Serengeti National Park or Ngorongoro Conservation Area in Loliondo and the NCA were sought respectively. In all cases, respondents were probed for their reasoning (Oppenheim 1992).

Impact of carnivores on Maasai

Following analysis of risk perception, quantification of actual confrontation was recorded. Unlike the questions on attitudes, when confusion between species could say much about perceptions, it was important that the respondent knew which species was being discussed during this section. Therefore, if any doubt had been demonstrated over the identification of each species in the previous section the interviewer firstly clarified which species was which. Most commonly, confusion occurred between cheetahs and leopards. Therefore, using the photographs for illustration, cheetahs were described as thinner predators, occasionally seen in groups and usually active in the day whilst leopards were described as being stockier, usually seen alone, often found in trees and usually active at night. Three aspects of conflict were then investigated. Firstly, the frequency of contact between Maasai and each species was assessed, secondly accounts of attacks on livestock were investigated and thirdly accounts of attacks on people were recorded. This section of the interview was based on single, open questions (Oppenheim 1992), asking when a given species was last sighted by the respondent, when his livestock were last attacked and whether anyone in his boma had been attacked. Questions on human attacks were based at the boma level because initial surveys demonstrated that human attacks were too rare to gain many positive responses when restricted to the respondent or his *olmarei* only. This also allowed verification by other respondents from the same boma. If any answer was positive, the respondent was then invited to elaborate on the details. If they were not mentioned he was prompted for the location, time of day, season and further details of the encounter. This was repeated for each of the main carnivore species. Ideally, quantification of conflicts with the carnivores would be based on number of incidences per year. However, initial interviews demonstrated that most people could not reliably remember all incidents, or were not comfortable basing estimates on a calendar unfamiliar to many Maasai. Therefore, frequency was estimated by asking the last time an incident occurred. Frequency was then coded as either within the last day, within the last week, within the last month, within the last year, more than a year ago or never, to give a relative estimate of timing.

Impact of Maasai on carnivores

Questions used to determine the impact of the Maasai on the carnivores were based on two issues. Firstly, they were questioned on the direct impacts on carnivores through killing, either through defensive or active hunting actions. Secondly, indirect effects were assessed by investigating the level of herbivore hunting and possible competition for carnivore prey resources. Since persecution and hunting of wild animals is an incredibly sensitive issue, especially in an area such as the Serengeti ecosystem where conservation issues are highly publicised and hunting without a permit is illegal, assessing the level of persecution of predators by Maasai is extremely difficult. If it does occur to any level, it is not in the respondent’s interest to answer truthfully, for fear of retribution. Therefore, initially a more indirect approach was taken, avoiding direct and potentially accusative questions and asking questions sympathetically in terms of the boma and village in general rather than the respondent himself. The first question asked whether people in the boma needed to use poison or snares to control the predators. If the answer was negative, the respondent was asked why not. If positive, the respondent was asked how frequently they were used, when was the last use and whether it had been successful. However, preliminary surveying in Loliondo demonstrated that, surprisingly, most people would talk openly about contentious issues. Further questions were therefore more direct, asking if the respondent had ever killed a predator himself and if so, how many. Secondly, respondents were asked about the lion hunt or “*olamayo*”, asking how many they had been on themselves and how many lions their *manyatta* had been responsible for killing. Respondents were then asked if they ever hunted any other kinds of animals. If so, they were asked further details on frequency, species and weapon use. If not, they were asked why.

Re-visit interviews

Due to the problems of quantifying the frequency of predator conflict, the main interviews were supported by a supplementary survey that revisited interview respondents and repeated the questions on livestock losses and gains, attacks by predators on livestock and people and predator persecution. However, respondents were asked for details only on incidents that had occurred since the previous visit, thereby giving a fixed reference point in time allowing more accurate quantification of the frequency of conflict.

Event diaries

In addition to re-visit questionnaires, diaries were also used to obtain a more accurate estimate of frequency of stock losses, attacks on people, carnivore persecution and lion hunts over a given period and to verify interview reports. Diaries were handed to a trusted representative of each village who then kept a record of all relevant events in the village he heard of over one year. To ensure all relevant data were collected for each event, the diaries were pre-drawn into columns and simply required filling in when appropriate (Table 64).

Table 64 - Information collected in village diaries

Lion hunt		Predator attacks	
English	Swahili	English	Swahili
Date	Tarehe	Date	Tarehe
Number of people	Idadi ya watu	Time	Wakati
Success	Matokeo	Attacker	Mnyama mkali
Area hunted	Mahali	Witnessed?	Wameona?
Names of any injured	Jina ya watu walijejeriuhi	Male / female	Dume / jike
Name of *murran* who claims kill	Jina ya mtu aliyeuwa simba	Livestock type	Aliyeshamelewa
Notes	Maelezo mengineo	Killed / injured	Kuuwa / kujeriuhi
		Area	Mahali
		Name of owner	Jina
		Boma name	Jina ya boma
		Notes	Maelezo mengineo

Lion hunt (*olamayo*) interviews

Information on lion hunts was collected in the main interview survey. However, preliminary survey rounds showed that the *olamayo* was still an important part of Maasai culture. Therefore, a separate investigation was conducted to determine its cultural significance and estimated impact on the lion population. The *olamayo* is traditionally carried out by the current *murran* age set, divided into *manyatta*s and led by a *laigwanan* or traditional leader, with *manyatta* successes displayed at the *eunoto* end of age set ceremony (see Chapter 1: Introduction). Lion hunt interviews were therefore aimed at the *laigwanan* of each previous age set to gather historical data and at the current *murran* to gain information on present day lion hunts. Interviews were structured very loosely, with prompting questions to ensure the essential details were covered, but generally respondents were encouraged to talk freely about the *olamayo* to avoid the restrictions and preconceptions of a rigid interview structure. Firstly, the interviews determined the age set of the respondent and the size and extent of the age set. Secondly, open questions were asked on the role of the *laigwanan*, followed by a description of the *olamayo* process from preparation to celebration of the kill. Further details were gathered on the trophies taken and their fate. The impact of the *olamayo* was then assessed, asking details on the number of lions killed by individual *manyattas* and on the successful hunters within the age set.

Analysis was carried out using χ^2 contingency tables to compare frequencies of responses for most questions, using a Yates correction factor when only one degree of freedom was available (Zar 1999). A generalised linear model was used to analyse livestock losses (see Methods chapter). All analysis was carried out using SPSS (SPSS Inc. 2001) and Genstat (Lawes Agricultural Trust 1996)

Survey effort

179 full interviews were conducted, each taking about one hour to complete. 53 re-visit interviews, 3 village diaries and 11 lion hunt interviews were also completed. 112 of the main interviews were carried out in Loliondo from four primary villages and six opportunistically visited villages. The target sample sizes were met for all villages except Soit Sambu, which was six interviews short. 67 were carried out in the NCA from two primary villages and six opportunistically visited villages (Table 65).

66% of interviews in Loliondo and 16% in the NCA were carried out by me. All others were carried out by translators following careful training.

Table 65 – Summary of villages visited and total interviews carried out

Loliondo Game Controlled Area		Ngorongoro Conservation Area	
Village	No. interviews	Village	No. interviews
Ilchoroi	1	Indiyau	9
Kirthalo[1]	2	Leboi Soit	4
Maloni	1	Naiborsoit	1
Munderosi[1]	3	Nasiporeng	19
Olobo	1	Neliyau	1
Ololosokwan	22	Olbalbal	3
Olopiri	23	Oljoke	2
Olorien	32	Olmekeke	28
Olorsirwa[1]	22		
Soit Sambu	5		
Total	112		67

[1] Sub-villages of Soit Sambu

7.4 Results

Demographic parameters

Regional divisions and age sets

In all areas, the sections represented, their constituent age sets, together with the estimated ages in years of their constituents and age set *laigwanan*, were determined by talking to elders. Four sections were represented in the study area (Table 66).

Table 66 – Maasai sections represented in the study area and a list of villages representing each section

Section	Region	Villages
Purko	Loliondo	Olorsiwa, Ololosokwan, Mairoa, Kilthalo, Mapongonyi, Munderosi, Irijoroi (Kenya)
Iloitai	Loliondo	Olorien (partial), Magaduru, Arash, Maloni, Olobo
Ilaitayok[1]	Loliondo	Olopiri, Okuini, Soit Sambu (Okoroi bomas[2]),Olkuyani (near Olopiri), Sukenya, Oldonyo Wass, Olkiu, Olorien (partial), Silale
Kisongo	Ngorongoro	All villages in the NCA study area

[1]Known for being more partial to hunting than other clans

[2]Main site for clan celebrations

Age division titles varied with section, but *olaji* (joined names) were universal across Loliondo. However, *olaji* names differed for the NCA Kisonjo section. Furthermore, unlike Loliondo sections, the Kisonjo had *olaji* titles for the younger age divisions, presumably because it is generally the Kisonjo that lead other sections undergoing the *olngesher* or unifying ceremony (Spencer 1993). Most of the Purko *laigwanan* were interviewed but few *laigwanan* from other sections were traced. Particular effort was made with Kisonjo *laigwanan* but in almost every attempt the target respondent was absent from his home boma (

Table 67 - Table 70). In Loliondo, most respondents were from the age set aged roughly between 20 and 40 (Ilbaluka and Ilkishili). However, in Ngorongoro this group was much less heavily represented. The *murran* age set was relatively well sampled in Loliondo but few were traced for interview in Ngorongoro (Figure 48).

Table 67 - Purko section *laigwanan*

Olaji (age set)	*Olporror* (age division)	*Laigwanan* name (+ home village)	Approx. ages	Interviewed
	Ilmeshuke	None (still open)	15-18	
Not joined yet	Ilbulka	Ketende Ole Ngoitoe (Munderosi)	18-30	Y
	Ilkishili	Samau Ole Rotteken (Oloika)	30-37	Y
Ilkitoipi	Ilrangang	Koinari Ole Toroge (Mairoa)	38-42	N
	Ilkisaya	Kaisaine Ole Sumari (Mairoa)	42-50	Y
Seuri	Iltiyongoni	Sandete Ole Reiya (Munderosi)	50-55	Y
	Iltirekeyani	Terede Ole Karea (Kenya)	55-60	N
Nyongrasi	Elkamanigi	Lekshon Ole Ngotiko (Lorsiwa)	60-65	Y
	Elkalkal	Dead	65-80	N

Table 68 - Loitai section *laigwanan*

Olaji (age set)	*Olporror* (age division)	*Laigwanan* name (+ home village)	Ages	Interviewed
	Ilmeshuke	None (still open)	15-18	
Not joined yet	Ilbulka	Lengrumu Ole Parmiria (Orngarwa, nr. Loliondo)	18-30	N
	Ilkishili	Kashanga Ole Pusalet (Olorien)	30-38	N
Ilkitoipi	Ilrandai	Leken Ole Parsambey (Olorien)	38-42	N
	Ilkisaya	Kalanga Ole Naronyo (Olobo)	42-50	Y
Seuri	Irmaoya	Ole Ngoet (Arash)	50-55	N
	Iltirekeyani	Rokoini Ole Sarora (Maloni)	55-60	N
Nyongrasi	Elkamanigi	Ole Kesindo	60-65	N
	Elkalkal		65-80	N

Table 69 - Laitayok section *laigwanan*

Olaji (age set)	*Olporror* (age division)	*Laigwanan* name (+ home village)	Ages	Interviewed
	Ilmeshuke	None (still open)	15-18	
Not joined yet	Ilbulka	Lepason Ole Kelande (Soit Sambu)	18-30	N
	Ilkishili	Shangai Ole Putaa (Soit Sambu)	30-38	N
Ilkitoipi	Ilrandai	Ikayo Ole Mbalala ((Olkuyani)	38-42	N
	Ilkisaya	Ololuare Ole Loru (Olkiu)	42-50	N
Seuri	Iltiyongoni	Oleleseyo Ole Parmes (Sukenya)	50-55	N
	Iltirekeyani	Olemoneyo Ole Sonye (Oldonyo Wass)	55-60	N
Nyongrasi	Elkamanigi	Siparu Ole Membe (Soit Sambu)	60-65	Y
	Elkalkal	Dead	65-80	N

Table 70 - Kisonjo section *laigwanan*

Olaji (age set)	*Olporror* (age division)	*Laigwanan* name (+ home village)	Ages	Interviewed
Ilmerishe[1]	Konanga	Ole Kelanga	15-18	Y
Ilkidotu / Kingande[2]	Ilbuluka	Lekini Ole Misori (Ngorongoro)	18-30	N
	Ilkishili	Lerati Ole Mbokotia (Makaromba)	30-38	N
Ilkishomu / Makaa	Ilkolonjon	Ndasikoi Ole Nakoroi (Indian)	38-42	N
	Makaa	Mberius Ole Renya (Endulen)	42-50	N
Seuri	Iltchurogo	Olmulee Ole Siwandette (Endulen)	50-55	N
	Ilcholik	Simon Ole Naseya (Endulen)	55-60	N
Ilmeshuke	Elkamanigi	Ole Nduyoto (Olbalbal)	60-65	N
	Elkalkal	Ole Ndeuni (Olbalbal)	65-80	N

[1] Although already given a joined name used by most respondents, the *olngesher* ceremony has not yet been performed therefore the unification is unofficial.

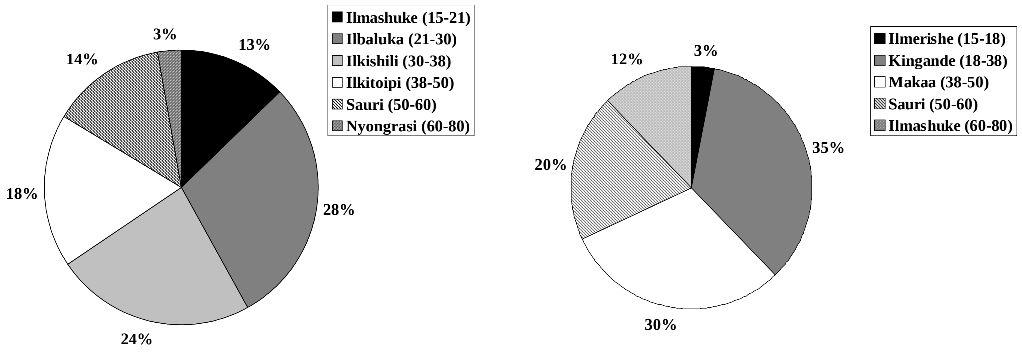
[2] Two *olaji* names were recorded because one was given by elders when describing the age set names but the other was more commonly used by respondents

To avoid confusion in further analyses due to variation of age set and subdivision names in different sections all age divisions were then re-named to a single standard (Table 71).

Table 71 – Standardisation of section age division names for use in analysis

Olaji (joined age set name)	*Olporror* (sub divisional name)	Approximate ages (yrs)
Ilmashuke	Ilmashuke	15-18
Kingande	Ilbaluka	18-30
	Ilkishili	30-37
Ilkitoipi	Ilrangrang	38-42
	Ilkisaya	42-50
Sauri	Iltiyongoni	50-55
	Iltirekeyani	55-60
Nyongrasi	Elkamanigi	60-65
	Elkalkal	65-80

Figure 48 - Distribution of ages sets / divisions interviewed



Loliondo

Ngorongoro

Social and economic status

Olmarei and boma composition

Comparisons of household sizes in each region was confused by the fact that boma in Ngorongoro were not divided into *olmarei* divisions. Therefore, Loliondo respondents gave the numbers of people in their *olmarei* whilst respondents in Ngorongoro estimated the number of people in their entire boma. However, using the number of *olmarei* in each Loliondo boma surveyed, the Loliondo data could be used to estimate the mean number of people per boma in Loliondo and these results were compared with NCA results using a z-test as appropriate for data with more than 30 samples (Fowler & Cohen 1990).

Table 72 – Social make up of Maasai *olmarei* and bomas in Loliondo and Ngorongoro

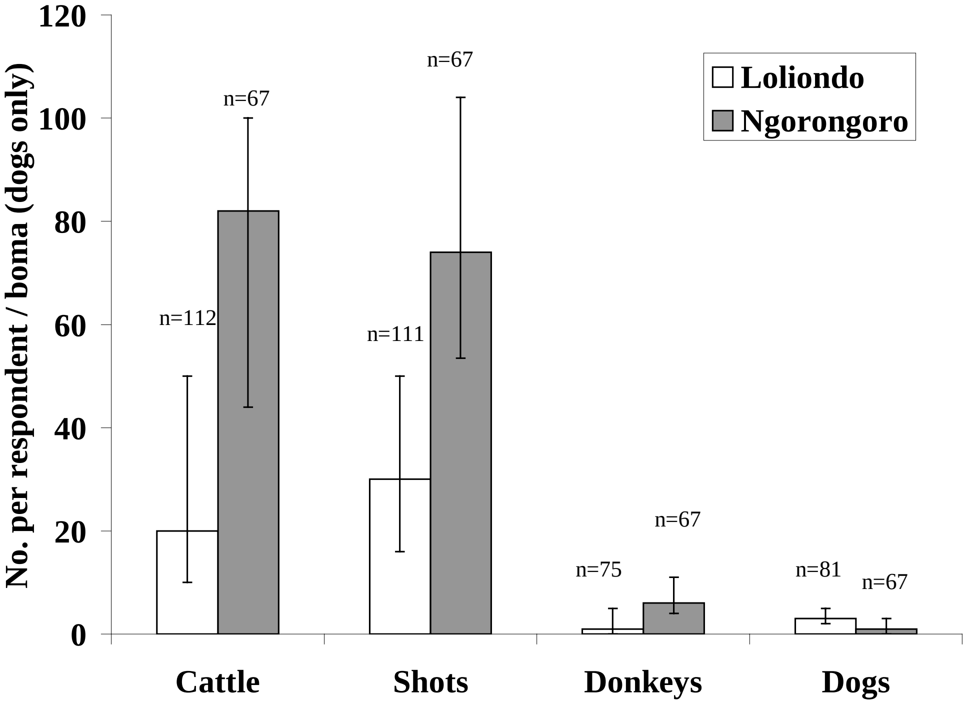
		Loliondo (n=110)		Ngorongoro (n=66)	
		Mean	SE	Mean	SE
Mean no. per *olmarei*	Men	3.3	0.2	-	-
	Women	4.3	0.3	-	-
	Children	9.6	0.3	-	-
	Mean no. *olmarei* per boma	4.5	0.3	-	-
Mean no. per boma	Men	15.0	1.6	6.21	1.0
	Women	19.4	2.6	12.1	1.1
	Children	43.0	5.4	27.5	2.0
	Total	77.4	9.5	45.8	4.1

Differences between total number of men per boma were significant (Z test: *Z*=2.32, p<0.005) but differences between number of women, children and total people per boma in each region were not significant.

Animal holdings and crop use

Livestock holdings ranged greatly, from zero to over 400 cattle and 600 sheep and goats. Respondents from Ngorongoro were wealthier than those from Loliondo, with significantly more cattle (Mann-Whitney U test: *Z*=-6.56, p<0.001), sheep and goats (*Z*=-5.44, p<0.001) and donkeys (*Z*=-5.65, p<0.001) but bomas in Loliondo contained more dogs (*Z*=-4.47, p<0.001) (see Figure 49). Crop use was high and similar in both regions. In Loliondo, 89% of respondents reported growing crops to supplement their income from livestock (n=73). In Ngorongoro, 81% reported growing crops (n=67).

Figure 49 - Median values of livestock owned by respondents and number of dogs per boma in each region. Shots refer to sheep and goats combined. Bars represent interquartile ranges.



Attitudes towards carnivores

Initial impressions of carnivores

Maasai perceptions of carnivores as a valid grouping

177 respondents free-listed wildlife present in their region, with 112 representing Loliondo and 65 representing Ngorongoro. On average, respondents mentioned 11-12 (mean=11.6) species and in total 45 wildlife species or categories were suggested. Perceptions of the carnivores as a distinct grouping were tested by measuring the average distance apart that species appeared within the lists and using this measure of association to plot a multidimensional scale plot. The plots show that lions, leopards and hyaenas were usually mentioned close together in lists in both Loliondo and Ngorongoro (Figure 50 and Figure 51). Lions and leopards were the most closely associated pairings of all the commonly mentioned species. However, jackals were far more loosely associated with the larger carnivores and cheetahs and wild dogs showed no association at all. The two major groupings in each area appeared to represent those species most common in the area (gazelles, wildebeest and zebra) together with

those most likely to pose a threat (lions, leopards, hyaenas, buffalo and elephant in Ngorongoro) with the second grouping comprising most of the species mentioned only once or twice. The free-lists suggest that using the western definition of carnivores as a basis for interviews is valid for the Maasai, but cheetahs and wild dogs do not appear to be major components.

Figure 50- MDS plot of relative distances between the order of mention during free-listing in LGCA. The further apart animals are, the less frequently they were mentioned together in lists.

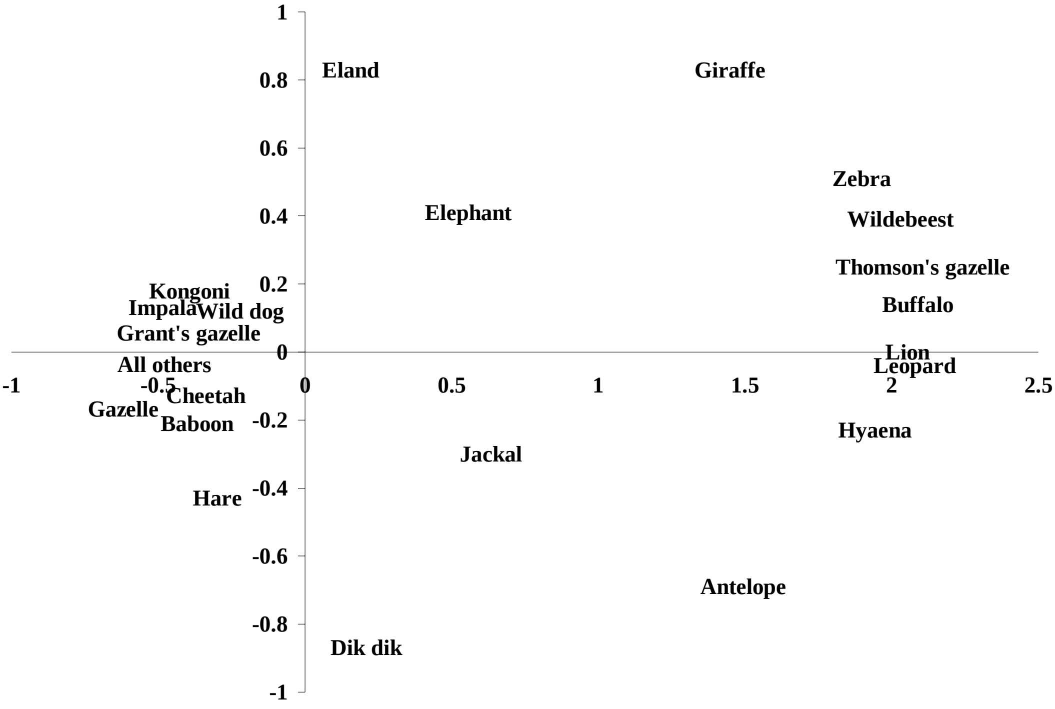
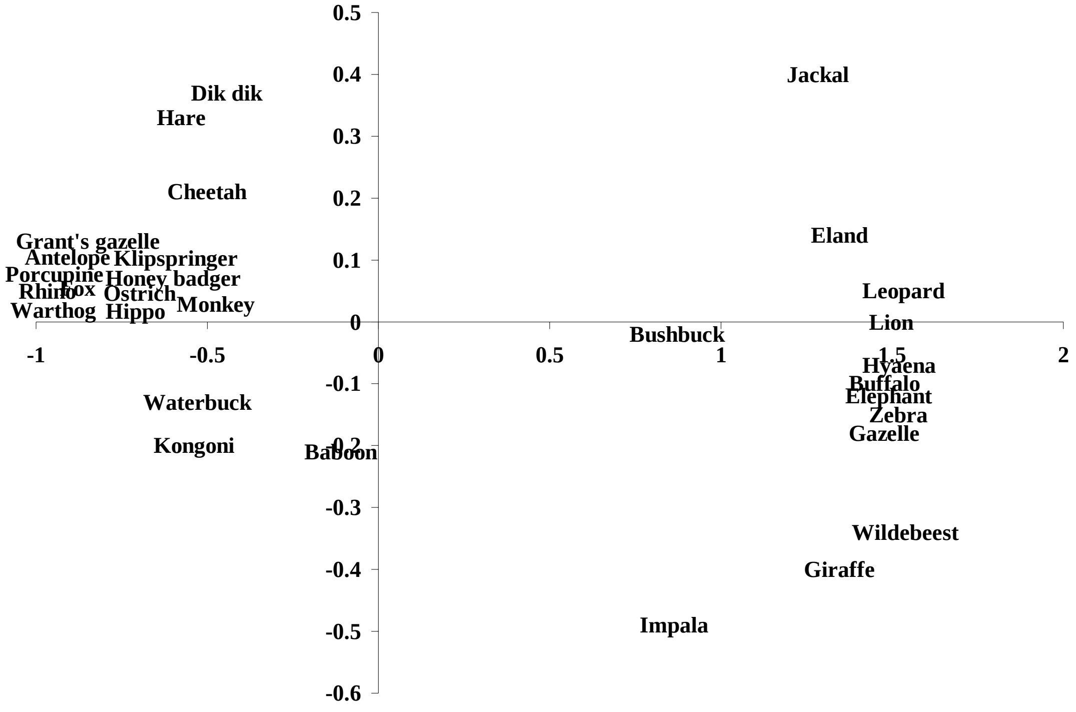


Figure 51 - MDS plot of relative distances between the order of mention during free-listing in NCA. The further apart animals are, the less frequently they were mentioned together in lists.



Salience of carnivores in relation to other species

Salience scores of all species mentioned showed that lions, hyaenas and leopards were the most important carnivores mentioned, with buffalo, wildebeest and zebra the most important of the herbivores. Cheetahs were rarely mentioned and usually later in the lists.

Table 73 – Species free-listed by respondents in Loliondo and Ngorongoro, showing the relative frequency each was mentioned and the saliency index. The list is ordered by the overall saliency index value.

	% respondents mentioning			Saliency index		
	Loliondo	Ngorongoro	Overall	Loliondo	Ngorongoro	Overall
Lion	91.1%	86.2%	89.3%	0.61	0.60	0.61
Buffalo	89.3%	86.2%	88.1%	0.58	0.66	0.61
Zebra	80.4%	92.3%	84.7%	0.48	0.53	0.50
Hyaena	75.9%	93.8%	82.5%	0.42	0.59	0.48
Leopard	86.6%	84.6%	85.9%	0.49	0.45	0.47
Wildebeest	81.3%	81.5%	81.4%	0.46	0.44	0.45
Elephant	40.2%	89.2%	58.2%	0.25	0.65	0.39
Giraffe	64.3%	78.5%	69.5%	0.32	0.40	0.35
Eland	37.5%	73.8%	50.8%	0.18	0.41	0.26
Thomson's gazelle	80.4%	7.7%	53.7%	0.38	0.04	0.25
Antelope	64.3%	4.6%	42.4%	0.32	0.03	0.21
Jackal	43.8%	67.7%	52.5%	0.16	0.22	0.18
Gazelle	12.5%	87.7%	40.1%	0.04	0.37	0.16
Impala	17.0%	60.0%	32.8%	0.06	0.18	0.10
Dik dik	37.5%	30.8%	35.0%	0.11	0.05	0.09
Cheetah	12.5%	23.1%	16.4%	0.07	0.11	0.09
Bushbuck	2.7%	53.8%	21.5%	0.01	0.17	0.07
Kongoni	17.9%	20.0%	18.6%	0.06	0.06	0.06
Baboon	16.1%	38.5%	24.3%	0.04	0.07	0.05
Hare	24.1%	23.1%	23.7%	0.06	0.02	0.04
Wild dog	18.8%	0.0%	11.9%	0.07	0.00	0.04
Grant's gazelle	13.4%	3.1%	9.6%	0.03	0.03	0.03
Warthog	9.8%	10.8%	10.2%	0.02	0.04	0.03
Waterbuck	1.8%	20.0%	8.5%	0.01	0.06	0.03
Fox	7.1%	1.5%	5.1%	0.02	0.00	0.02
Hippo	5.4%	3.1%	4.5%	0.02	0.01	0.02
Snake	5.4%	1.5%	4.0%	0.02	0.00	0.01
Ostrich	3.6%	6.2%	4.5%	0.00	0.03	0.01

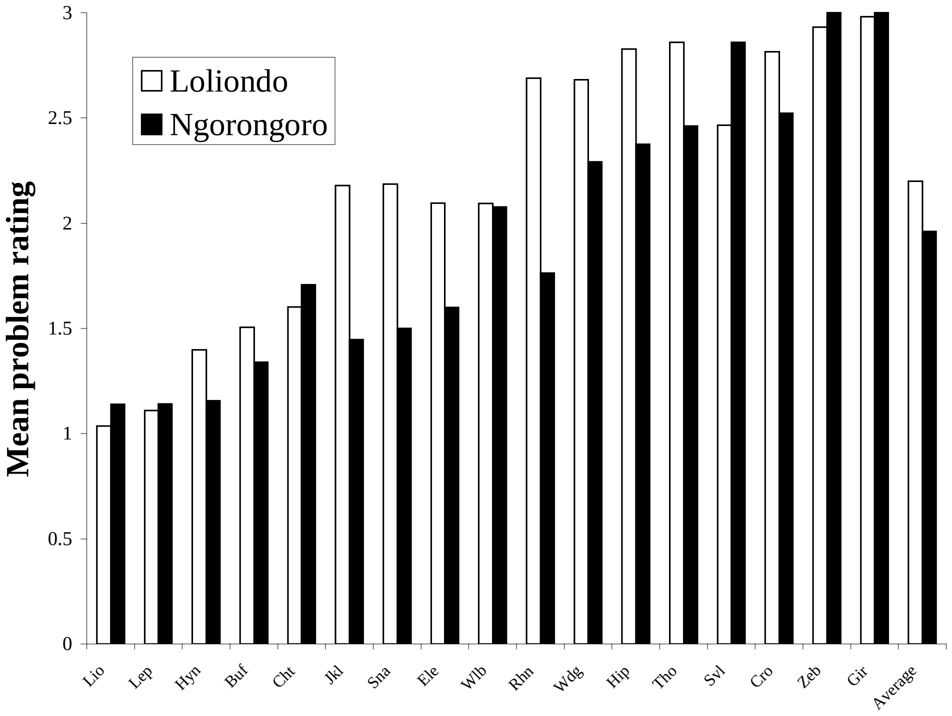
	% respondents mentioning			Saliency index		
Monkey	8.0%	1.5%	5.6%	0.01	0.00	0.00
Birds	4.5%	0.0%	2.8%	0.01	0.00	0.00
Klipspringer	1.8%	1.5%	1.7%	0.00	0.00	0.00
Topi	1.8%	0.0%	1.1%	0.00	0.00	0.00
Reedbuck	1.8%	0.0%	1.1%	0.00	0.00	0.00
Wild cat	0.9%	0.0%	0.6%	0.00	0.00	0.00
Springhare	0.9%	0.0%	0.6%	0.00	0.00	0.00
Porcupine	0.9%	3.1%	1.7%	0.00	0.00	0.00
Fish	0.9%	0.0%	0.6%	0.00	0.00	0.00
Rhino	0.9%	1.5%	1.1%	0.00	0.00	0.00
Tortoises	0.9%	0.0%	0.6%	0.00	0.00	0.00
Steinbuck	0.9%	0.0%	0.6%	0.00	0.00	0.00
Striped hyaena	0.9%	0.0%	0.6%	0.01	0.00	0.00
Oryx	0.0%	1.5%	0.6%	0.00	0.01	0.00
Kudu	0.0%	1.5%	0.6%	0.00	0.01	0.00
Honey badger	0.0%	1.5%	0.6%	0.00	0.00	0.00

Perceptions of carnivores as problem species

Carnivores as problem species in relation to other wildlife

Examining the mean scores within each region based on picture pile sorts (with big problems scoring 1, small problems scoring 2 and no problems scoring 3) shows large carnivores were the top scoring species, headed by lions, leopards and hyaenas but followed by buffalo and cheetah. Scores were similar in both regions for most species, except that most species were rated as slightly more problematic in Ngorongoro, especially jackals, snakes, rhinos and elephants (Figure 52).

Figure 52- Representation of relative Maasai perceptions of problem status of carnivores in relation to other species. Low scores = larger problem.



Perceptions of individual carnivore species

Discussing pictures of each of the main carnivores showed that lions were almost universally recognised (Table 74). 97% of respondents that answered the question in Loliondo (n=108) and 100% in Ngorongoro (n=65) gave the Maa name of *ongatung*, the only exceptions being elderly respondents with eyesight too poor to see the cards. Hyaenas had similarly high recognition value, with only 4% of respondents identifying them incorrectly. However, the name used by the Purko in Ngorongoro was *orugojine*, a name that refers to their apparently shorter back legs, but *okonoi* in Loliondo. However, identification of leopards and cheetahs was far less precise. Most respondents labelled both as *olowaru kheri*, which translates as the spotted predator. When pushed to differentiate, many respondents in Ngorongoro were able to divide the two into *orkelusa*, the leopard, and *orkedi*, the cheetah, but in Loliondo fifteen possible names for the cheetah were given, many of which translated into appropriate descriptions. Recognition of wild dogs, on the other hand, was high, with most respondents recognising them as *osieni*, although some confusion occurred with jackals.

Table 74 – Summary of % respondents giving various Maa names for photographs of each of the main predators, together with a rough English translation when known.

	Maa name	English translation	Loliondo	Ngorongoro
			% respondents answers	
Lion	*Ongatung*	Lion	97	100
	Other		3	0
Hyaena	*Orugojine*	Short legged predator	1	97
	Okonoi	Hyaena	93	3
	Osuiani	Wild dog	3	0
	Olowaru kheri	Spotted predator	1	0
Leopard	*Olowaru kheri*	Spotted predator	78%	66%
	Orkelusa	Leopard	0%	28%
	Olkinyo lasho	Calf predator	15%	0%
	Olowaru	Predator	1%	0%
	Ongatung	Lion	1%	0%
	Olowaru orok		1%	0%
	Orkedi	Cheetah	0%	6%
	Don’t know		1%	0%
	Other		3%	0%
Cheetah	*Olowaru kheri*	Spotted predator	61%	48%
	Osipilwa	Thin predator	10%	0%
	Oltanaa	Serval	5%	0%
	Olowaru rangi	Thin predator	3%	0%
	Olongo serong	Creature of open areas	3%	0%
	Olowaru keri kiti	Small spotted predator	2%	0%
	Olowaru le Angata	Predator of open areas	2%	0%
	Olkinyo Lasho	Calf predator	2%	0%
	Olokelul	Thin one	1%	0%
	Simanggi	Fast runner	1%	0%
	Mpus	Domestic cat	1%	0%
	Olowaru		1%	0%
	Olowaru ngusi		1%	0%
	Olowaru oibor		1%	0%
	Ormara		1%	0%
	Osonombo		1%	0%
	Olowaru lengulin	Thin predator	0%	5%
	Orkelusa	Leopard	0%	5%
	Orkedi	Cheetah	0%	37%

	Maa name	English translation	Loliondo	Ngorongoro
	Olchui	Bastardized Maa / Swahili - leopard	0%	2%
	Orkerasi		0%	2%
	Don't know		3%	2%
	Other		3%	0%
Wild dog	*Osieni*	Wild dog	86%	91%
	Nemele	Striped hyaena	2%	0%
	Obari	Jackal	2%	0%
	Osiro	Jackal	1%	0%
	Okonoi	Hyaena	1%	0%
	Oldya	Domestic dog	1%	0%
	Enderash	Jackal	0%	2%
	Don't know		5%	8%
	Other		3%	0%

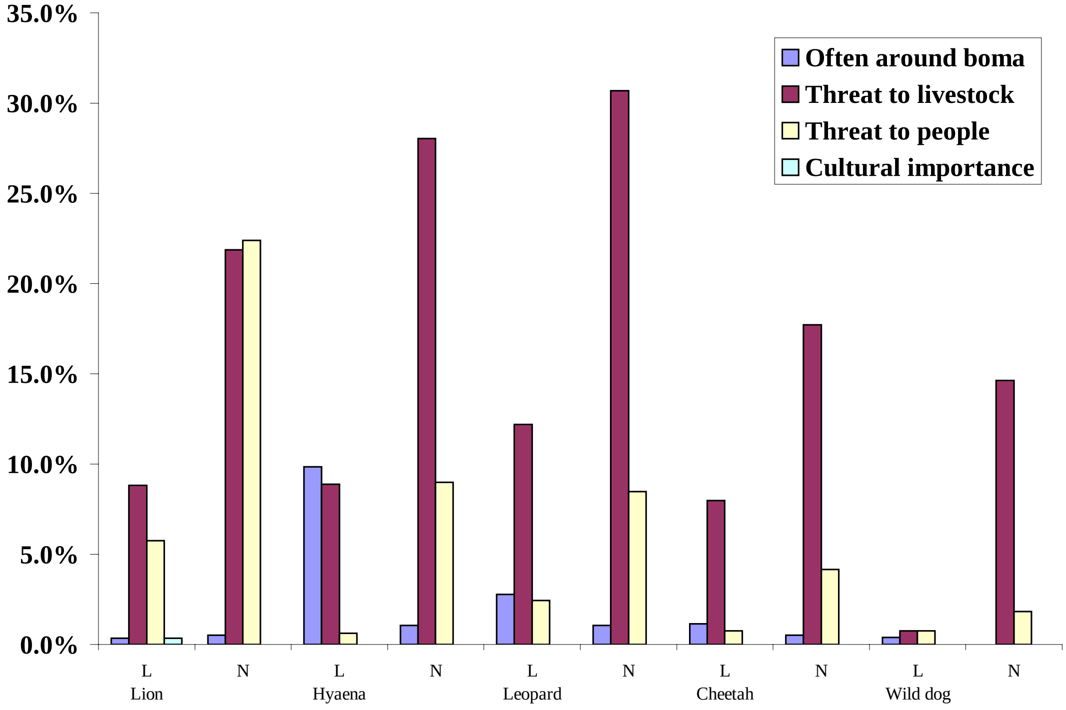
Table 75 - % frequency of descriptions of each carnivore species given by respondents in Loliondo and Ngorongoro.

	Lion		Hyaena		Leopard		Cheetah		Wild dog	
	$\chi^2_3=54.26$, $p<0.001$)		$\chi^2_3=67.03$, $p<0.001$)		$\chi^2_3=37.81$, $p<0.001$)		$\chi^2_3=17.07$, $p<0.05$)		$\chi^2_3=36.15$, $p<0.001$)	
	Lol	NCA	Lol	NCA	Lol	NCA	Lol	NCA	Lol	NCA
Often around boma	0.3% (1)	0.5% (1)	9.8% (31)	1.1% (2)	2.8% (8)	1.1% (2)	1.1% (3)	0.5% (1)	0.4% (1)	0.0% (0)
Threat to livestock	8.8% (26)	21.9% (42)	9.2% (29)	28.0% (53)	11.9% (34)	30.2% (57)	8.0% (21)	17.7% (34)	0.8% (2)	14.6% (24)
Threat to people	5.8% (17)	22.4% (43)	0.6% (2)	9.0% (17)	2.4% (7)	8.5% (16)	0.8% (2)	4.2% (8)	0.8% (2)	1.8% (3)
General description	85% (250)	55.2% (106)	80.3% (253)	61.9% (117)	82.9% (237)	60.3% (114)	90.1% (237)	77.6% (149)	98.1% (260)	83.5% (137)

All statements that were descriptive (*e.g.* "eat meat") were discarded from the analysis and comparisons were made of only the frequency of conflict-related statements. Differences between perceptions of each species (Table 75, Figure 53) were significantly different in both regions (Loliondo: $\chi^2_{12}=120.4$, $p<0.001$, NCA: $\chi^2_{12}=82.2$, $p<0.001$), with lions particularly associated with livestock predation and human predation and hyaenas, leopards and cheetah associated less with human predation but more with associations with the boma and livestock predation. Comparing descriptions of cheetah and leopards only were insignificantly different in

Loliondo (χ^2_3=7.17, *NS*) but they were different in Ngorongoro (χ^2_3=13.4, $p<0.05$). In general, respondents in Ngorongoro were far more likely to make conflict-related statements about the different species.

Figure 53 – % Frequency of descriptions of primary predator species given by respondents in Loliondo (L) and Ngorongoro (N). Only results for descriptions related to conflict with people are presented. The frequencies of generally descriptive comments are not plotted.



General attitudes towards wildlife and protected areas

Positivity towards wildlife

General attitudes towards wildlife and the environment were investigated by asking what respondents thought about having wild animals living near them, whether they would like any animals to be controlled and what they thought of the Serengeti National Park or Ngorongoro Conservation Area. In response to “What do you think about having wild animals living around here?” respondents in each region gave significantly different answers (χ^2_3=93.0, $p<0.001$) with only 5% of Loliondo respondents reporting wildlife was a bad thing in general compared to nearly three quarters of respondents in Ngorongoro (Table 76). However, the remaining responses in Loliondo were not wholly positive with over 40% giving a non-committal response of “good and bad” or did not have an opinion. Nevertheless, the majority of Loliondo respondents thought wildlife was good in general, compared to just 20% in Ngorongoro.

Table 76 – Relative frequency of general attitudes towards wildlife together with explanations. Actual frequencies are given in parentheses.

Response	Explanation	Loliondo	Ngorongoro
Bad		5%(5)	74% (48)
	Disease risk	19%	47%
	Competition with livestock	5%	20%
	Threat to livestock / crops / people	67%	33%
	Conflict with other users	10%	0%
Good		53% (57)	20% (13)
	Economic	68%	73%
	Hunting	9%	0%
	Aesthetic / cultural	20%	9%
	Provision of lions for *olamayo*	3%	0%
	Alternative food for carnivores	0%	18%
Good and bad	Reasons included above	24% (26)	6% (4)
No opinion	No reasons given	18% (19)	0% (0)
	Total replies	107	65

Differences in reasons for opinions were not tested significantly due to low frequencies in some categories. However, the data show that by far the main reason given for negative attitudes in Loliondo was the threat to livelihoods or lives, followed by the risk of disease and conflict with other users (commercial hunters and photographic tour companies were both named by various respondents). In contrast, Ngorongoro respondents rated disease as the most important reason for negative attitudes, followed by the threats to livelihoods and lives. Furthermore, the perception of wildlife as competitors for grass was a more commonly cited reason than in Loliondo. Differences in the importance of other users of wildlife stem from two specific organisations operating in Loliondo that have come into conflict with certain villages.

Control of wildlife

38% respondents in Loliondo (n=73) would like to see someone control wildlife to some degree in their area, compared with 77% (n=66) of respondents in Ngorongoro. Of the Loliondo respondents, several answering “yes” to control qualified this by suggesting that only leopards needed to be controlled (Table 77). Attitudes towards control in each region were significantly different ($\chi^2_1=21.4$, $p<0.001$) with many more respondents in Ngorongoro stating a desire for wildlife to be controlled.

Table 77 – Attitudes of respondents towards control of wild animals

Would like someone to control wildlife?	Region	
	Loliondo	Ngorongoro
Yes	38.4% (28)	77.3% (51)
No	61.6% (45)	22.7% (15)

Attitudes towards the protected areas

Table 78 – Attitudes towards the protected areas and the reasons given

Opinion	Reasoning	Loliondo	Ngorongoro
Negative		15% (16)	18% (12)
	Management	0%	100%
	Lack of profit	23%	0%
	Grazing restrictions	77%	0%
Positive		42% (45)	79% (52)
	Management	2%	0%
	Freedom	0%	60%
	Aesthetic / ethical / history	8%	13%
	Hunting opportunities	2%	0%
	Indirect economic	16%	2%
	Grazing	4%	6%
	Conservation	20%	0%
	Employment	8%	6%
	Prevention of raids	16%	0%

Opinion	Reasoning	Loliondo	Ngorongoro
	Direct benefits	10%	13%
	Benefits for country	16%	0%
Mix opinions	Reasons included in relevant category above	2% (2)	0% (0)
No opinion	No reasons given	41% (44)	3% (2)
No. respondents giving opinion on protected areas		107	66
No. respondents giving reasons		64	59

Comparisons between attitudes towards protected areas in Loliondo and Ngorongoro are not strictly applicable since each was asked a different question (attitudes towards the Serengeti National Park and NCA respectively). However, comparisons were made to provide an indication of attitudes towards local protected areas. Differences of positive and negative responses between Loliondo and Ngorongoro were significant (χ^2_2=101.1, $p<0.001$ – “mixed” opinions and “no” opinions were combined for the analysis to avoid any cells being below 5) with many more respondents in Ngorongoro expressing positive attitudes towards the NCA.

The reasons given for each attitude were not analysed statistically since several categories including less than five respondents and there was no meaningful way of amalgamating. However, reasons for negative attitudes were evidently different in each region, with Loliondo respondents primarily complaining of the effects on grazing (either the loss of grazing due to the gazetting of the park or current restrictions on taking livestock into the park) whereas Ngorongoro Maasai without exception attributed negative attitudes to problems with management, either referring to rules placed on them or in some cases specifying a perception that the NCA authority valued wildlife above people. Reasons for positive attitudes in Loliondo were primarily based on economic reasoning, either direct, as perceived for others, as employment or in the national interest. However, the other primary reason given, which accounted for more than any other single reason, was the benefit respondents perceived going to conservation and wildlife, with similar aesthetic or ethical reasons also an important determinant. A third important reason, which was unique to

Loliondo, was the role the National Park provided as a barrier with the Wasakuma people to the west, thus reducing conflict and cattle raiding.

Reasons for the benefits of protected status in Ngorongoro also heavily featured economic benefits (although no mention of the national interest was made) and some ethical responses referring to the importance of history and heritage were also important. However, most respondents answered that the protected area was good as it allowed “freedom”.

Impacts of carnivores on Maasai

Frequency of interactions with carnivores

Timing of most recent sightings

Plotting the distribution of most recent sightings of each carnivore and assuming the timing of sightings is related to frequency, it can be seen that sightings frequencies were significantly different from each other in both Loliondo ($\chi^2_{20}=382.5$, $p<0.001$) and Ngorongoro ($\chi^2_{20}=390.3$, $p<0.001$). Hyaenas were the most frequently sighted, seen by 60% of respondents within the last twenty four hours and over 90% within the last month. Only one respondent stated he had never seen a hyaena. Lions were the next most commonly sighted, with over 70% respondents reporting having seen one within the last month and nobody reporting to have never seen one. Sightings of leopard were more recent than cheetah, with 50% reporting sighting one in the last month compared to 35% reporting a cheetah sighting and over 20% stated they had not seen a cheetah in over a year compared to 16% for leopards. Wild dogs were the least frequently sighted carnivore, but sightings were far more recent than initially expected considering their extinction from the Serengeti, with 9% reporting sightings in the last month and over 30% reporting having seen them in the last year. Testing the differences between sightings frequencies in each region showed no differences in sightings of lions ($\chi^2_4=2.87$, *NS*), hyaenas ($\chi^2_5=9.76$, *NS*) or wild dogs ($\chi^2_4=6.5$, *NS*) but cheetahs were seen significantly more recently in Ngorongoro ($\chi^2_5=25.0$, $p<0.001$) as were leopards ($\chi^2_5=19.3$, $p=0.002$).

Figure 54 - Distribution of most recent sightings reported for each of the main carnivore species in Loliondo. All distributions were significantly different except cheetahs and leopards.

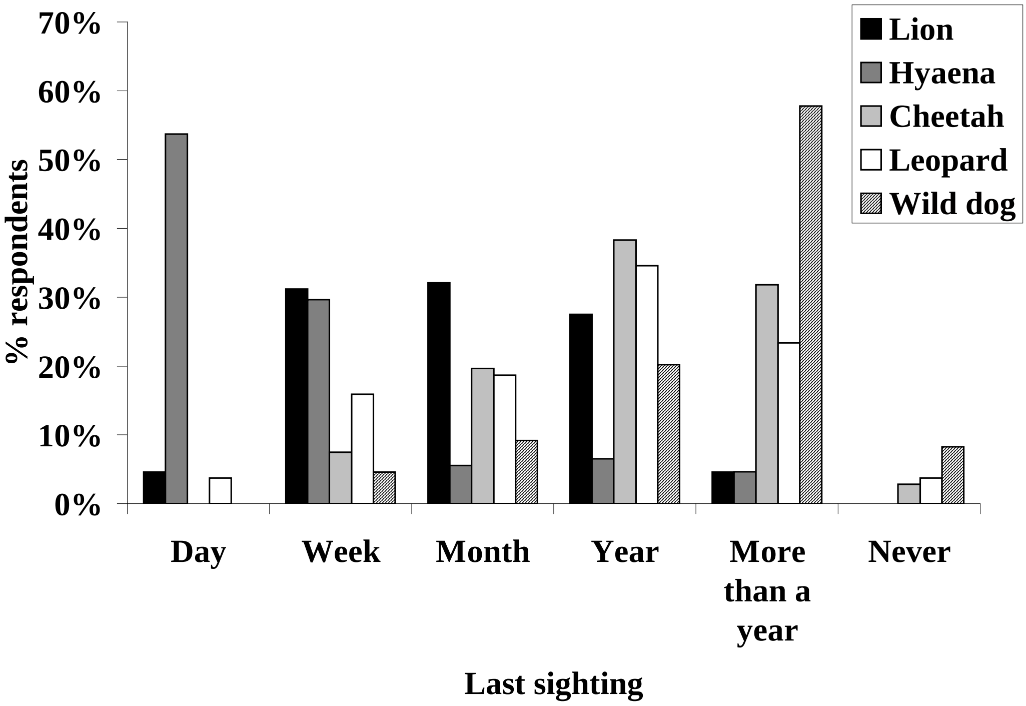
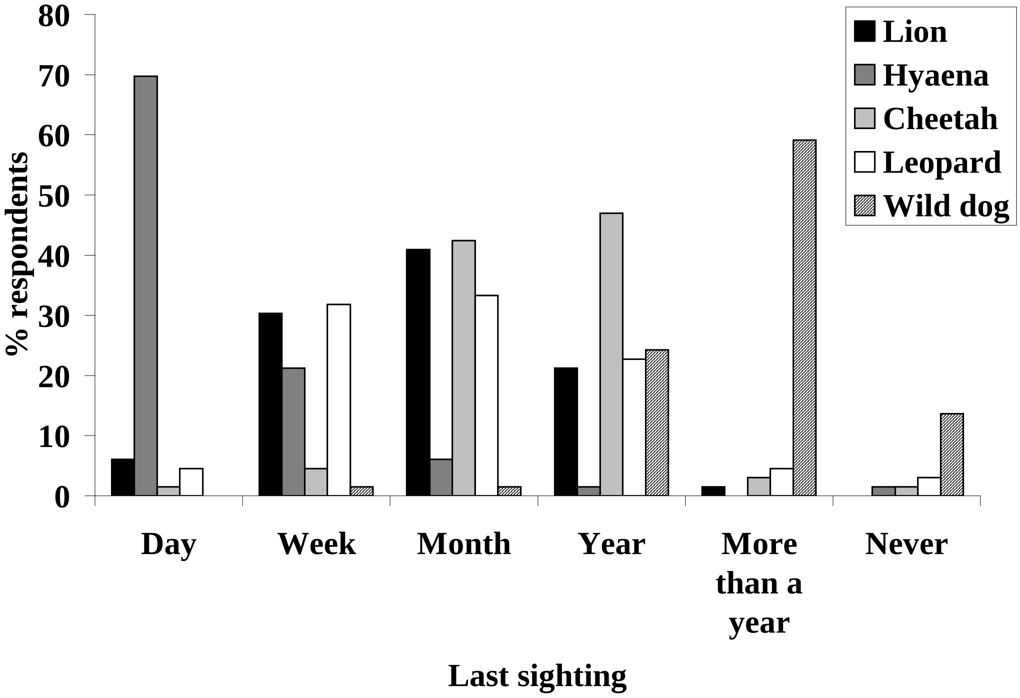


Figure 55 - Distribution of most recent sightings reported for each of the main carnivore species in Ngorongoro. All distributions were significantly different.



Impacts of carnivores on Maasai livestock

Level of livestock losses

The majority of respondents in both regions experienced at least one attack on their livestock at some point of their lives (Table 79), with significantly more respondents in Loliondo reporting attacks than in Ngorongoro ($\chi^2_2=17.8$, $p<0.001$).

Table 79 – Proportion of respondents reporting an attack by a predator on their livestock at some point in their life

	Loliondo	Ngorongoro
No. respondents	110	66
Never experienced attack by any predator	10.7% (12)	37.3% (25)
Experienced at least one attack by a predator	89.3% (98)	62.7% (41)

To quantify losses, respondents were also asked the numbers lost in the previous month. In an attempt to account for difficulties in timing when remembering events, these data were compared with data from revisiting some respondents in Loliondo and asking the number of livestock lost since the previous visit (Table 80). Re-visit interviews were generally conducted 1 month after the previous visit (median=34 days) and losses adjusted to represent losses per month (31 days). Unfortunately, statistical comparisons between revisit and general interviews were not possible since revisits usually stated that no livestock had been lost. However, the data that were available suggested that estimates of losses based on re-visits were much lower than estimates made by first time respondents.

Table 80 – Mean % herd reported lost to predators in the previous month

		Interviews		Re-visits	
		Cattle	Shots	Cattle	Shots
Loliondo	% of herd	1.16 (±0.44)	4.44 (±1.08)	0.75 (±0.26)	0.35 (±0.62)
	Total	0.38 (±0.11)	1.15 (±0.31)		
Ngorongoro		0.74 (±0.24)	1.49 (±0.41)		
	Total	0.58 (±0.21)	0.93 (±0.25)		
Average		0.96 (±0.26)	3.06 (±0.62)	0.75 (±0.37)	0.35 (±0.27)

To investigate the differences between losses in Loliondo and Ngorongoro whilst controlling for other potentially explanatory factors the numbers of livestock lost in the previous month (as estimated by normal interviews since revisits were not carried out in Ngorongoro) as a proportion of the total herd owned were modelled against the region, season, type of livestock guard and whether other people were present during the interview. A generalised linear model was used (see Chapter 2) specifying binomial errors as appropriate for proportional data (Crawley 1993). The results for losses of cattle (Table 81) showed that region was the only significant factor explaining variation in losses, with Ngorongoro reporting more losses but Loliondo showing higher losses as a proportion of cattle owned (GLM: χ^2_1=5.3, p<0.05)

Table 81 – Factors affecting cattle losses to predators

Factor	Degrees of freedom	χ^2	Probability
Region	1	5.3	0.021
Season	1	1.4	0.237
Boys or men herding	1	0.3	0.584
Others present	1	0	1.000

Losses of sheep and goats, however, were insignificantly different between the two regions but significantly explained by season (χ^2_1=4.4, p<0.05), with more occurring in the dry season, and by the guard identity (χ^2_1=3.9, p<0.05), with most losses reported by those reporting the use of adults when guarding livestock as opposed to children.

Table 82– Factors affecting sheep and goat losses to predators

Factor	Degrees of freedom	χ^2	Probability
Season	1	4.4	0.036
Looks after	1	3.9	0.048
Others	1	0.1	0.752
Region	1	0	1.000

Losses to predators in the context of other herd dynamics

Herd dynamics were investigated by recording the total livestock owned at the time of interview and all losses and gains occurring in the previous month by 142 respondents. Cattle herds were reported to have been reduced by a mean of 15% (±3) and shots herds by 20% (±2) in Loliondo and 9% (±1) and 15% (±1) respectively in Ngorongoro over the month prior to interview (although these were total losses, not net loss, and were often compensated by increases in stock). Of the reasons for reductions of livestock, death by disease or “natural causes” and sale were the primary reasons, however, predation accounted for 5-10% of livestock reductions (Figure 56 and Figure 57)

Table 83 – Reasons for cattle herd reductions

	Loliondo	Ngorongoro
Sold	29.1 (285)	33.9 (140)
Died	44.8 (439)	38 (157)
Slaughtered	7.7 (75)	1.9 (8)
Gifts	10.0 (98)	13.1 (54)
Stolen	3.3 (32)	0.5 (2)
Predation	2.9 (28)	9.4 (39)
Other	2.2 (22)	3.1 (13)

Reasons given for reductions in cattle herds were significantly different in each region (χ^2_6=60.1, p<0.001 - Table 84) with natural deaths (primarily disease) accounting for most losses in both regions, followed by sales. Losses through gifts and “other” reasons (lost, owed in debt *etc.*) were also similar. The main differences were due to predation, with Ngorongoro respondents reporting a higher percentage of losses, slaughtering (for ceremonies, celebrations or food), which was higher in Loliondo, and theft, which was also higher in Loliondo (Figure 56).

Table 84 – Reasons for shots herd reductions

	Loliondo	Ngorongoro
Sold	23.9% (330)	25% (199)
Died	34.5% (477)	23.2% (185)
Slaughtered	17.9% (248)	27.3% (217)
Gifts	9.3% (129)	14.7% (117)
Stolen	5.9% (82)	0.4% (3)
Predators	6.4% (88)	7.7% (61)
Other	2.1% (29)	1.8% (14)

Reasons for reductions in sheep and goat herd sizes were also significantly different between the two regions (χ^2_6=96.3, p<0.001 - Table 84). Patterns were similar to cattle in that sale and natural deaths were two of the major contributors to herd losses and like cattle, respondents in Loliondo suffered the highest proportion of losses due to death. The main differences were that many more shots were slaughtered in Ngorongoro during the period of questioning – in fact slaughtering was the primary cause of herd reduction. Gifts were also more common in Ngorongoro and again theft was only a problem in Loliondo. Losses due to predation and other reasons were higher in Ngorongoro but similar (Figure 57).

Figure 56 – Percentages of total cattle losses attributed to each potential cause in Loliondo and Ngorongoro

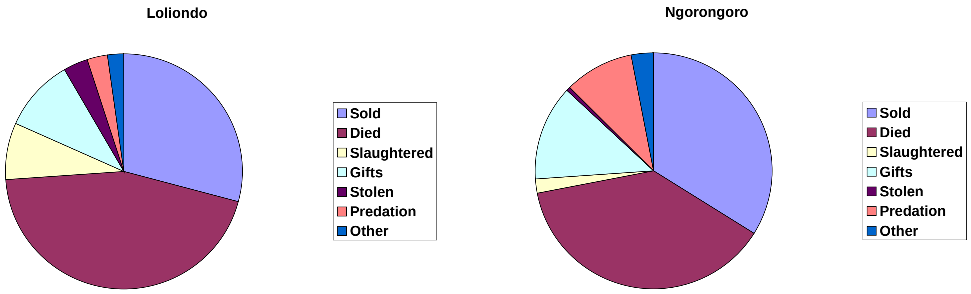
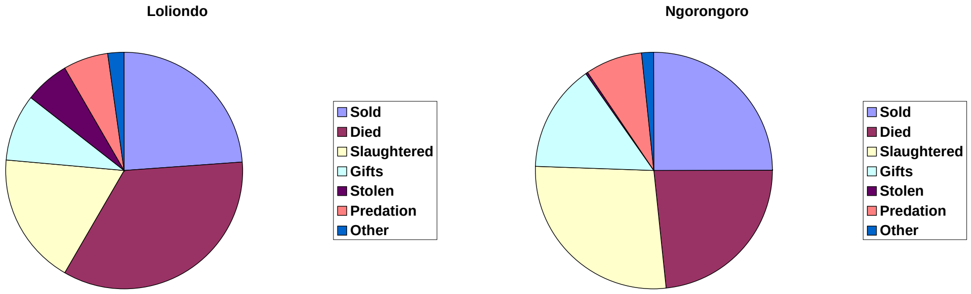


Figure 57– Percentages of total sheep and goat losses attributed to each potential cause in Loliondo and Ngorongoro



Predation accounted for significantly more of the reductions of cattle herds in Ngorongoro (Mann Whitney: Z=-1.98, p=0.048) but there was no significant difference between regions for sheep and goats (Mann Whitney: Z=0.846, p=0.397).

Carnivore species most commonly causing attacks on livestock

Far more respondents in Loliondo reported having suffered an attack by each of the predators, with over 80% reporting an attack at some point by either a leopard or a lion and over 70% reporting attacks by hyaenas (Table 85). However, the relative frequency of reports in each region (excluding wild dogs) was not significantly different (χ^2_4=1.61, *NS*), with lions, hyaenas and leopards the most frequently cited experiences of attacks.

Attacks by cheetahs were experienced far less often in both regions.

Table 85 – Proportion of respondents (total number of respondents) reporting attacks by each of the major predators

	Loliondo	Ngorongoro
Lion	85.6% (81)	40.9% (27)
Hyaena	71.7% (71)	28.8% (19)
Cheetah	13.0% (14)	10.8% (7)
Leopard	80.8% (84)	46.2% (30)
Wild dog	0.9% (1)	0.0% (0)

Frequency of attacks by different carnivores

Distributions of timing of the most recent attack by each predator species were significantly different in both Loliondo (χ^2_{20}=312.6, p<0.001) and Ngorongoro (χ^2_{20}=95.3, p<0.001) with hyaena and leopard attacks tending to be the most recent, followed by lions. Cheetah attacks were rarely reported recently if at all and wild dog attacks almost unheard of in both regions. Comparing the distributions of most recent attacks by individual species showed lions (χ^2_4=64.4, p<0.001), hyaenas (χ^2_5=54.6, p<0.001) and leopards (χ^2_5=53.4, p<0.001) were all significantly different in each region with a higher proportion of respondents in Ngorongoro never having experienced an attack. However, differences between cheetahs in each region were not significant (χ^2_4=9.0, *NS*).

Figure 58 – Distribution of timing of most recent attack reported by Loliondo respondents

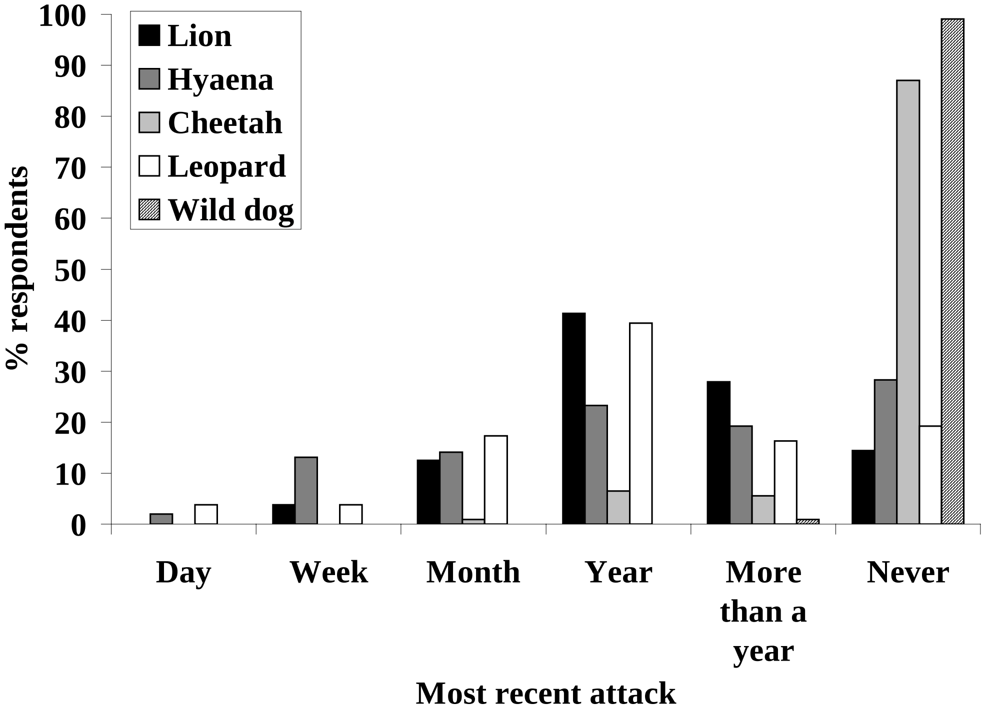
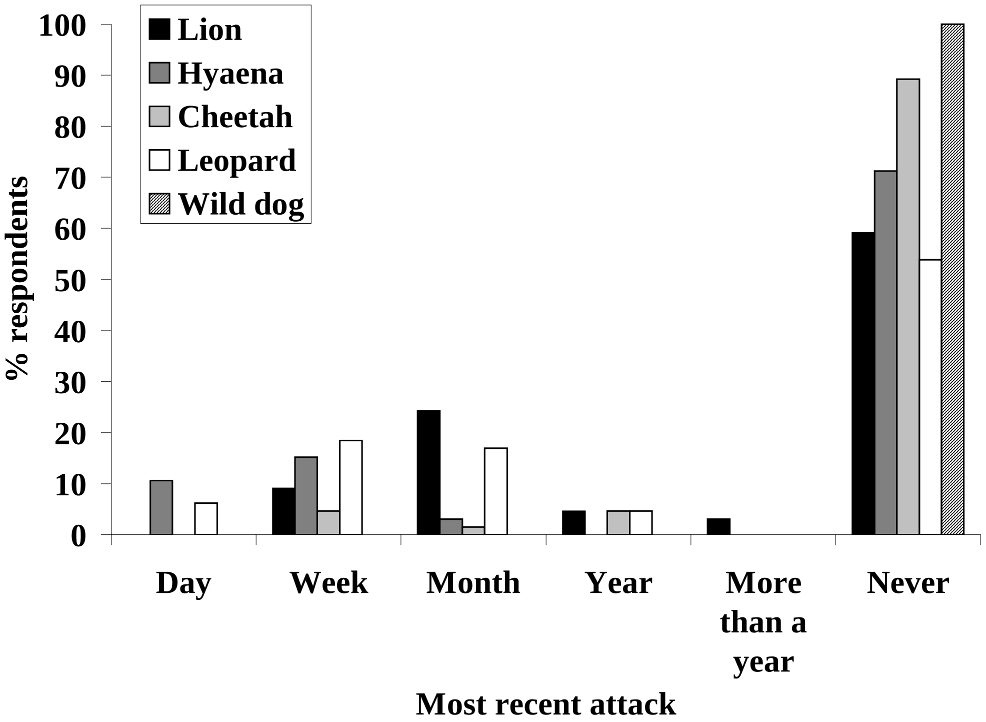


Figure 59 - Distribution of timing of most recent attack reported by Ngorongoro respondents



Data were also collected on the details of all attacks reported including the proportions of kills *vs.* injuries, time of day of attacks, method of attack and prey choices. Since these are not strictly relevant to the chapter hypotheses these can be found in Appendix V (p.368).

Human casualties

Relative frequency of attacks

Lions accounted for most of the reports of attacks by predators, with respondents from over one fifth of bomas visited reporting an attack at some point by a lion on someone in their boma. Attacks by hyaenas and cheetahs were negligible but attacks by leopards were also reported relatively frequently in Loliondo by respondents from 8% of bomas. Loliondo respondents reported a higher proportion of bomas experiencing attacks by lions, but the differences were not significant (χ^2_1=1.6, *NS*). Frequencies were too low to test for differences in other predators.

Table 86 – Proportion of bomas reporting experience of at least one human injury due to each predator

	Loliondo	Ngorongoro
Lion	21% (14)	13% (8)
Hyaena	1% (1)	0
Leopard	8% (5)	2% (1)
Cheetah	0	2% (1)

When possible, reports were checked with respondents from the same boma. The checks revealed that five of the reports of lion attacks in Loliondo and one report of a leopard attack were unsubstantiated by other respondents in the boma. In Ngorongoro one of the lion attacks and the cheetah attack were not substantiated by other members of the boma. Although these results may appear to cast serious doubt on the results it should also be added that in some cases respondents who claimed no attacks had occurred were re-visited at a later date and asked why their story did not match a previous respondent’s answer. In several of these examples, the original respondent then remembered the event and changed his account. In other words, the assumption that an attack by a predator would be a major event remembered by all in the boma did not appear to be the case. This could be because some of the accounts reported events from many years ago but it may also indicate that encounters with predators, especially during lion hunts, are effectively part of every day life.

Details on individual attacks

Respondents were asked what the victim was doing at the time of the attack for the two species for which attacks were relatively common (Table 87). Most of the victims of lion attacks in Loliondo were engaged in lion hunting at the time, with less than 30% attacked whilst going about daily business. A higher proportion in Ngorongoro was grazing cattle when attacked, but differences were not significant (χ^2_1=1.1, *NS*). In contrast, all attacks by leopards were incurred whilst either grazing or protecting livestock or, in Loliondo, inside or around the boma (following attacks on livestock) although frequencies were too low for statistical testing. The reports of injuries through hyaena attack occurred when the respondent was trying to chase hyaenas away, whilst the cheetah attack was said to happen whilst protecting livestock.

Table 87 – Proportion of respondents engaged in various activities during lion and leopard attacks.

Count of Activity	Lions		Leopard	
Region	Lion hunt	Grazing	Around boma	Grazing
Ngorongoro	50% (5)	50% (5)	0%	100% (1)
Loliondo	71% (10)	29% (4)	25% (1)	75% (3)

With one exception, none of the attacks reported by any predator resulted in the death of the victim. Furthermore, physical encounters with predators were undoubtedly infrequent, with over 80% (n=10) of the lion attacks happening over one year ago and most of those a decade or more ago. However, one attack was reported within the previous year and one attack was reported from the previous day. In this case, a twelve year old boy from Olorsiwa in Loliondo tried to drive a trio of lions from the herd he was tending. He was killed. A second case that was not picked up by the interviews occurred near the beginning of the study in one of the Loliondo study villages, whereby a rabid hyaena entered the village of Olorien and bit several people, including a young girl who received horrific injuries to her face. She was treated by the Flying Doctors service and her case is still used in promotional literature.

Impacts of the Maasai on the carnivores

Direct effects on carnivores

Use of snares or poison

Most respondents in both regions stated that they did not use either poison or snares with no difference between regions (χ^2_1=3.5, *NS*) (

Table 88), chiefly because they did not have access to any. Of the respondents that said they did use them, poison tended to be the most common form of indirect persecution, with several respondents mentioning the use of cattle dip to bait carcasses and one mentioning that poison was available in Kenya. Successes, when described, tended to involve hyaenas and jackals, although some claimed to have killed lions by poisoning carcasses. Snares were mentioned less frequently, although one respondent preferred them as they killed fewer animals. Breaking the results down by age group showed that the youngest and oldest respondents in Loliondo were more likely to use snares or poison, but these differences were insignificant (χ^2_4=6.5, *NS*). The very young were also more likely to use indirect persecution in Ngorongoro, but again differences were insignificant (χ^2_4=6.6, *NS*). Regions were compared by looking at the ages of all respondents that did use poison or snares. No differences were found between Loliondo and Ngorongoro (χ^2_4=5.6, *NS*) although values were too low for a very reliable chi-test. Furthermore, there was a direct contrast in the activities of the Nyongrasi age set, with Loliondo members all claiming to use snares or poison and Ngorongoro members all claiming not to. The frequency of use results show that most respondents in both regions only ever use in response to an incident with a very small proportion in Loliondo stating they use them on a regular basis. Values were too low to test statistically.

Table 88 – Proportion of respondents using poison and their reasons if given. Figures in brackets represent actual frequencies.

Do you ever use poison or snares?	Reasons if given	Loliondo	Ngorongoro
No	Don't have	83% (25)	88% (37)
	Don't need	13% (4)	5% (2)
	Not allowed	3% (1)	0%
	Don't want to	0%	7% (3)
Total No		**60% (59)**	**75% (47)**
Yes	For hyaenas	100% (1)	0%
	Threat to livestock	0%	100% (5)
Total Yes		**40% (39)**	**25% (16)**

Table 89 – Proportion of different age categories contributing to use indirect persecution of carnivores. Figures in brackets represent actual frequencies.

Age set (in order of age)	Loliondo		Ngorongoro	
	No	Yes	No	Yes
Ilmashuke	9% (5)	15% (6)	2% (1)	6% (1)
Kingande	59% (34)	53% (20)	30% (14)	50% (8)
Ilkitoipi	21% (12)	13% (5)	28% (13)	38% (6)
Sauri	12% (7)	11% (4)	24% (11)	6% (1)
Nyongrasi	0%	8% (3)	15% (7)	0%

Table 90 – Proportions of respondents reporting different frequencies of use of poison and/or snares. Values in brackets represent actual frequencies.

Frequency	Loliondo	Ngorongoro
In response to an incident only	75% (30)	100% (4)
1 / month +	13% (5)	0%
1 / year +	13% (5)	0%

Reports of direct carnivore persecution

Later in the questionnaire survey, it was apparent that respondents would talk openly about direct persecution of carnivores. Therefore, respondents were asked directly if they had ever killed a carnivore personally. Most (60%) respondents in both regions stated that they had (Table 91), with no difference between Loliondo and Ngorongoro (χ^2_1=0.11, *NS*). In Loliondo, no difference was seen between the age sets in the number claiming to have killed a predator (χ^2_4=7.6, *NS*), although older age sets tended to be more likely to have killed. Similar patterns were observed in Ngorongoro where the proportion claiming to have killed a predator increased significantly with age (χ^2_4=1.4, p=0.04), but this could be simply because they have had more time to do so.

Table 91 – Proportion of respondents claiming to have killed a predator in each region, divided by age set. Figures in brackets refer to actual frequencies.

Region	Age set (in order of age)	Ever killed a carnivore?	
		No	Yes
Loliondo	Ilmashuke	57% (4)	43% (3)
	Kingande	46% (22)	54% (26)
	Ilkitoipi	15% (2)	85% (11)
	Sauri	44% (4)	56% (5)
	Nyongrasi	0	100% (2)
Loliondo Total		**40% (32)**	**60% (49)**
Ngorongoro	Ilmashuke	100% (2)	0
	Kingande	57% (13)	43% (10)
	Ilkitoipi	42% (8)	58% (11)
	Sauri	36% (4)	64% (7)
	Nyongrasi	0	100% (8)
Ngorongoro Total		**42% (27)**	**59% (37)**

Table 92 – Mean numbers of each predator killed by respondents in each region

	Cheetah	Hyaena	Leopard	Lion	Wild dog
Loliondo	0.11 (±0.04)	0.40 (±0.11)	0.57 (±0.22)	0.62 (±0.11)	0.05 (±0.04)
Ngorongoro	0.02 (±0.02)	0.21 (±0.08)	0.32 (±0.12)	0.79 (±0.14)	0.00
Overall mean	0.07 (±0.03)	0.31 (±0.07)	0.46 (±0.13)	0.69 (±0.08)	0.03 (±0.02)

Differences between the numbers of each predator killed (Table 92) within each region were significant in both cases (Loliondo: Kruskal-Wallis: χ^2_4=44.8, p<0.001 and Ngorongoro: Kruskal-Wallis: χ^2_4=65.8, p<0.001) with lions being the most commonly killed, followed by leopards. Relatively few people reported ever having killed a cheetah or a leopard. Differences between the regions were not significant for any species (Kruskal-Wallis: χ^2_1=3.4 (cheetah), 2.4 (hyaena), 0.6 (leopard), 0.8 (lion), 1.6 (wild dog), all *NS*.

The lion hunt

Investigations into the *olamayo* or lion hunt were carried out by asking each respondent how many lion hunts he had attended and how many lions he thought his *manyatta* had killed. In addition, *laigwanan* (the traditional leaders of each age group) and current *murran* were interviewed to gain general information on the hunt process as well as estimates of the numbers of lions killed by their group. Unfortunately no *laigwanan* were traced in Ngorongoro so all *laigwanan* data are based on Loliondo sections.

Lion hunt structure and description

Initial analysis used the *laigwanan* interviews to build up a picture of the lion hunt process. Little variation was described and therefore an anecdotal summary is presented. During murranhood the *murran* are still divided into their *olporror* age divisions, with a *laigwanan* leading each. Once there are sufficient numbers initiated into a new age division all members from a given section (representing Maasai from Tanzania and southern Kenya for some of the Loliondo sections) are also divided into 2-5 *manyatta*s of 150 to 500 members each (depending on the size of the age cohort) with whom they live. During murranhood, members of each *manyatta* will carry out lion hunts, a process that, if successful, wins great local prestige as they parade the mane and occasionally tail, claws and skin around neighbouring bomas. However, the ultimate goal is to collect as many manes together, to make them into head-dresses and to compare with other *manyatta*s at the *eunoto* ceremony, held in Kenya for several sections, that marks the end of murranhood and transition into a junior elder.

There does not appear to be any rigorous structure to lion hunt initiation. Many of the respondents stated that a lion hunt simply begins when some *murran* decide that they want to go. Traditionally other *murran* are rallied using a kudu horn, but otherwise word of mouth is sufficient. An important point was that only *murran* ever hunt lions for prestige. Several respondents stated that if an older man was involved in killing a lion, he gained none of the prestige a *murran* received. This was supported by one of the older interview respondents who claimed to have recently killed an adult male lion. When asked why he could not show any evidence he said there was no point taking a mane if you were not a *murran*, adding people would laugh and think you were trying to act young again. Furthermore, not all *murran* can go on an *olamayo*, with the older *murran* deciding who can and who cannot. Generally, younger or smaller *murran* are told they cannot attend. The numbers of *murran* that go on a single hunt varied with respondents, but generally groups of 10-30 *murran* were described. Hunts usually leave very early in the morning. Contrary to some reports, no stimulants or other chemicals were reported to be used and the only weapons taken were spears and *rungwas*, the small knob-kerrie clubs carried by many Maasai. To find a lion most reported heading to open areas with rivers (which are generally dry for most of the year but have thicker vegetation where animals can hide). Almost all the *laigwanan* from any section identified *Ang'ata kheri*, the open area where much of this ecological study was based, as the best area. Some specified that the forests were not used as the cover made it too difficult to find lions and too dangerous if they were found. The hunting party then divides into three groups, one on each bank of the river and one in the middle and they then search until a lion is flushed out. Sometimes this can take several days, with the *murran* either staying in the bush or calling on nearby bomas for shelter overnight. Once a lion is seen the *murran* use bells to chase it. The noise often makes the lion stop and turn on its pursuers. According to the *laigwanan* the method of killing is then to surround the lion in a circle and close in, all making as much noise and trying to be as intimidating as possible as the lion will then try and break out of the circle at the point with the least dangerous looking *murran* (a choice that is apparently humiliating to the individual chosen!) However, listening to some of the descriptions by *murran* recently returning from hunts suggested a less organised affair with no time to arrange circles and wait for an attack. It is at this point that the other *murran* attack, with the first to spear it claiming the mane. Some reported the second to spear claimed the tail; others claimed it was the first to cut it off. However, if anyone is seriously wounded in the attack no trophy is taken and no prestige is won. During these hunts it is the adult male lion that provides the great prestige, but most respondents agreed that other lions or species were hunted during an *olamayo*, either for practice in the case of other carnivores, or for shield skins in the case of buffalo. Only one *laigwanan* said female or young lions were not killed.

Lion hunt frequency

Table 93 – Proportion of respondents ever having been on a lion hunt with actual frequencies in brackets.

Region		No	Yes
Loliondo	Imashuke	27% (3)	73% (8)
	Kingande	15% (6)	85% (35)
	Ilkitoipi and older	10% (2)	90% (19)
All		15% (11)	85% (64)
Ngorongoro	Imashuke	50% (1)	50% (1)
	Kingande	41% (9)	59% (13)
	Ilkitoipi and older	17% (6)	83% (30)
All		26% (16)	74% (45)

Lion hunts are still a common practice in the survey area, with 80% of all respondents reporting that they had been on at least one when a *murran,* (Table 93) and no significant difference between the two regions (χ^2_1=2.8, *NS*). The proportion of respondents having attended a lion hunt tended to increase with age, although this was not significant in either region (Loliondo: χ^2_2=1.75, p=0.416, *NS*, Ngorongoro: χ^2_2=4.7, p=0.096, *NS*) The number of hunts attended by each respondent ranged from 0 to over 20, with the mean for each age set summarised in Table 94. Differences in the overall number of hunts carried out in each region were significant (Mann-Whitney: Z=-4.1, p<0.001) with more hunts reported in Loliondo. Differences can also be seen between age sets in Loliondo, with the number of lion hunts attended increasing with age. However, this effect was not significant in either Loliondo (Kruskal-Wallis: χ^2_4=8.1, p=0.09) or Ngorongoro (Kruskal-Wallis: χ^2_4=4.9, *NS*).

Table 94 – Mean number of lion hunts attended by each age set in each region

Region	Age set (in ascending age order)	Mean no. lion hunts (±SE)
Loliondo	Ilmashuke	1.57 (±0.65)
	Kingande	4.73 (±0.76)
	Ilkitoipi	7.08 (±1.99)
	Sauri	7.50 (±2.78)
	Nyongrasi	8.00 (±2.00)
	Overall mean	5.19 ±(0.66)

Ngorongoro	Ilmashuke	0.50 (±0.50)
	Kingande	2.05 (±0.67)
	Ilkitoipi	2.28 (±0.39)
	Sauri	1.75 (±0.59)
	Nyongrasi	2.00 (±0.37)
	Overall mean	2.00 (±0.3)

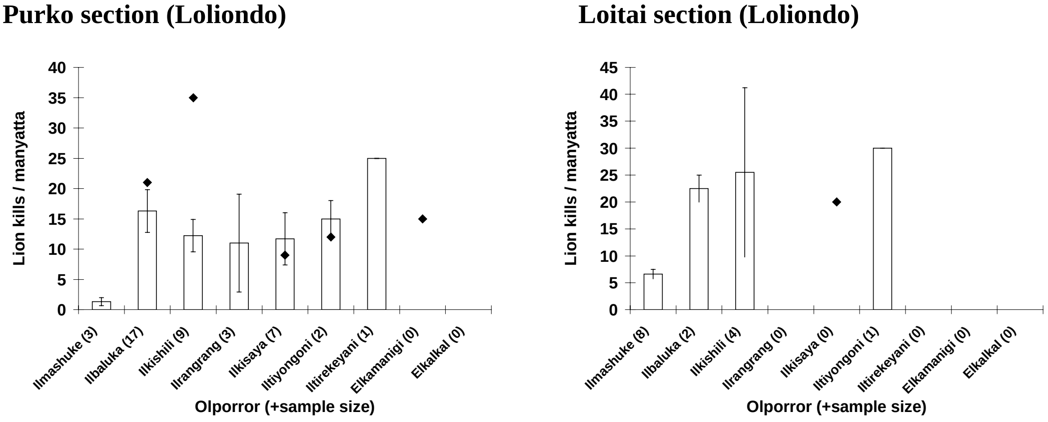
Fate of lion trophies

All but one of the *laigwanan* or *murran* respondents interviewed (n=12) stated that lion trophies could be sold to either tourists at the *eunoto* ceremony in Kenya, tourists in Loliondo or other Maasai. Expected prices for a mane ranged from £50 - £200 ($35 -$170).

Number of lions killed by lion hunts

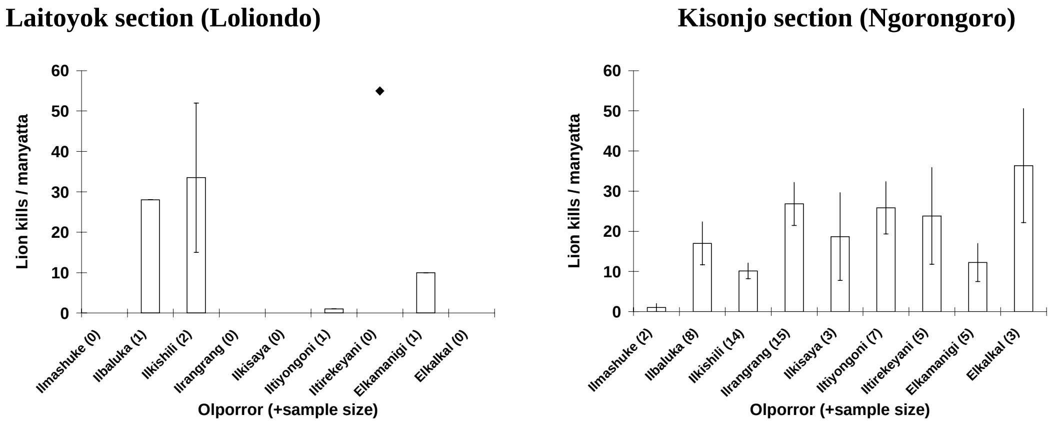
To estimate the numbers of lions killed by lion hunts, each respondent was asked the number of lions killed by his *manyatta* to give an estimate of the number of lions taken per *manyatta* for each age set subdivision. These results were then compared with figures given by *laigwanan* of each age division, with the expectation that the *laigwanan* was the most likely to know how many lions were killed in his group, although only *laigwanan* of the Purko section were traced in any number (Figure 60).

Figure 60 – Mean estimates of number of lions killed per *manyatta* in each age subdivision (*olporror*) of each section. Bars represent mean estimates based on general respondent interviews (±SE) whilst diamond markers represent the estimate given by the *olporror* leader (*laigwanan*)



Purko section (Loliondo)

Loitai section (Loliondo)



Laitoyok section (Loliondo)

Kisonjo section (Ngorongoro)

The results show estimates in the region of 10-20 lions per *manyatta* for most recent age divisions of the Purko and Kisonjo sections for whom most data were collected, and over 20 lions per *manyatta* by the Loitai and Laitoyok sections. Assuming an average of 4 *manyatta*s per *olporror* (based on a sample size of 11 *laigwanan* interviewed) and a cycle of *olporror* every seven years (Galaty 1993) these data suggest approximately 30-40 lions are being killed by lion hunts per year in the area covered by the four sections represented (covering Ngorongoro, Loliondo and southern Kenya).

These results can be compared with the with *laigwanan* answers on lion hunt frequency and event diaries of current Ilmashuke lion hunts kept by two respondents in Olopiri (Laitayok), one in Olorien (Loitai) and one in Olorsiwa (Purko). All *laigwanan* said lion hunts only ever occurred in the wet season because lions migrated to the Serengeti in the dry, because there was less work to do with livestock and also because it was easier to see their prints. Estimates of frequency were given by five of the respondents, each saying approximately twice a month during this period or 5-6 per year. The diaries showed that three successful lion hunts were carried out by Olopiri *murran* in the previous year (supported by both diarists), six had been carried out from Olorien and two from Olorsiwa. The Olorsiwa diarist also recorded unsuccessful hunts, showing six hunts had been attempted during the period.

Indirect effects on carnivores

One of the major threats to carnivores in some areas is competition with humans for prey sources (see Chapter 1, 3). Traditionally Maasai do not hunt wild animals for food but each respondent was asked, “Do you ever hunt wild animals (not including carnivores)?”. If positive, they were asked their reasons and further details. The results (Table 95) showed that herbivore hunting did occur in both Loliondo and Ngorongoro, but to a significantly greater extent in the former (χ^2_1=38.2, p<0.001). The reasons given for not hunting were primarily cultural (including “we have no need”, “we do not eat” or “don’t want to”) with a small number stating laws as their primary reason. The reasons for hunting were primarily for recreation in Loliondo and were mostly accounted for by *murran* hunting (see

Table 96). The other main reasons were for food, including two respondents who said they hunted to feed their dogs, and for pest control. This included zebras and Thomson’s gazelles for threatening maize crops but also buffaloes as threats to humans and cattle. Several respondents described how buffaloes would attack domestic cattle. In addition, one Iltiyogoni *laigwanan* listed a variety of ways Maasai used wildlife as a resource including lions for hunting, buffalo for shield skins, wildebeest tails as fly swats and zebra skin for binding arrow flights (respondent # 7). Estimates of frequency (

Table 96) showed that hunting was a relatively rare event with most in Loliondo saying it was very occasional, or that they had only ever hunted when a *murran*. Only one respondent stated he hunted regularly (to feed himself). Only two Ngorongoro respondents gave frequencies of hunting, estimating it was no more than once a year. Data on reasons and frequency were insufficient to apply statistical tests for differences. Finally, respondents were also asked what weapons they used when hunting. Every single respondent who answered said a traditional weapon such as spear or bow and arrow. No reports of firearm use were heard.

Table 95 – Proportion of respondents practising or abstaining from hunting herbivores together with reasons if given. Figures in brackets represent actual frequencies.

Do you ever hunt herbivores?	Reasons if given	Loliondo	Ngorongoro
No	Culture	97% (29)	97% (57)
	Law	3% (1)	3% (2)
No total		**44% (36)**	**92% (61)**
Yes	Food	24% (9)	0%
	Fun	55% (21)	20%(1)
	Pest control	21% (8)	75% (4)
Yes total		**56% (46)**	**8% (5)**

Table 96 – Approximate frequency estimated by respondents who said they did hunt herbivores

Frequency	Loliondo	Ngorongoro
Once a week+	3% (1)	0%
Once a month+	23% (9)	0%
Once a year+	15% (6)	100% (2)
Very occasionally	30% (12)	0%
When a *murran*	30% (12)	0%

7.5 Discussion

Attitudes of Maasai towards the carnivores and their environment

Contrary to expectation, the general attitudes of the Maasai in this survey were not particularly positive towards the large carnivores and did not immediately suggest that coexistence with carnivores was based on any form of goodwill. Lions, hyaenas and leopards were generally perceived as a distinct group, with salience scores indicating they were an important part of the Maasai environment, as were buffalo. Lions, hyaenas and leopards also topped the lists of problem species, above any conflict with herbivore species, and were frequently described in terms of threats to the respondent's livelihoods and were also the main reasons for any negative feelings listed towards the park, especially in Loliondo. However, overall attitudes did not necessarily paint a completely bleak picture of the conceptual environment in which carnivores outside the parks would have to live. For example, attitudes towards wildlife in general, suggestions of controlling wildlife and the protected area system were generally very positive. In general therefore, the attitudes of the Maasai seem to be positive towards their environment, which are probably the key issues when considering potential for coexistence, but specific issues exist with carnivore problems. Positive attitudes, despite specific problems have been recorded in other studies *e.g.* (Infield 1988), (Sekhar 1998), although these were usually accounted for by specific benefits accruing from the resources such as revenue sharing. However, no formal compensation or revenue system is in place in either Loliondo or Ngorongoro (Parkipuny 1997).

Impacts of the carnivores on Maasai livelihoods

Coexistence with carnivores was not based on avoidance of conflict, with a high rate of interaction indicated by the frequency of sightings and impacts detrimental to both the Maasai and the carnivores. The investigation of the impact of carnivores on the Maasai showed that most respondents had suffered at least one attack on their livestock, which was probably a major contributing factor for the negative attitudes. Quantification was not very reliable, judging by comparisons with revisit data and the % of total losses predation accounted for, presumably due to a difficulty in remembering events from a given date (see "Limitations of the study" p.306).

However, the best estimate was that around 1% of herds was lost per month, or 12% per year. This is a high rate of loss compared to some other studies (*e.g.* 1-2% *per annum* on ranches in Kenya (Mizutani 1993), but not as high as others *e.g.* 18% p.a. losses were estimated due to snow leopards and wolves in Nepal (Mishra 1997). However, comparisons are limited by many studies reporting different measures of losses such as total numbers or proportion of *per annum* capita *e.g.* (Singh & Kamboj 1996), (Butler 2000). Numbers of losses reported were higher in Ngorongoro but accounted for significantly higher proportions of total herds in Loliondo. Attacks in Loliondo were unaffected by herder age or number of guards present for cattle. Attacks in Ngorongoro, on the other hand, were affected by the herder, with more men losing livestock than children. However, this could be because men take over herding for a while after losses, so when asked who looks after the cattle a different response was given. However, to put predation into context, it is not the main source of herd loss for the Maasai, with natural deaths (disease *etc.*) and sales accounting for a higher proportion of livestock dynamics, similar to findings in other studies *e.g.* (Mizutani 1993). Attacks on people were far less frequent and almost all were accounted for by Maasai initiating an attack on a predator. Nevertheless, serious attacks attributed to lions and hyaenas did occur during the duration of the study, and even a single death can have a major psychological influence on attitudes and behaviour (Sillero-Zubiri & Laurenson 2001). Despite this, risk to human life appeared to take second priority to concerns over livestock in most cases. For example, in the village where the hyaena attack occurred, many respondents still did not mention threats to humans in the descriptions of hyaenas, but their threat to livestock was frequently cited. Lions, leopards and hyaenas were the primary species responsible for conflict, broadly agreeing with other studies in Africa (*e.g.* (Mizutani 1993), (Frank 1998), (Butler 2000)).

Impacts of the Maasai on carnivores

Impacts of the Maasai on the large carnivores were varied, but coexistence was not occurring through a lack of interaction. Indirect persecution such as snare use or poisoning, thought to be the major contributor to carnivore deaths in some Serengeti buffer zones (Hofer *et al.* 1996), was probably not a major factor. However, this was due to a lack of availability rather than any ethical or moral reasons. Nevertheless, when quantifying frequency almost all respondents claimed to use such methods only in response to specific events, rather than as a preventative measure. Indirect effects such as competition for prey through hunting or land being cultivated were still very minor in both areas studied, although agriculture could be important in the future (Thompson 1998). Direct impacts on carnivores, such as hunting, were more important with most respondents claiming to have killed at least one predator at some point. This appeared to be more common amongst the *murran*, and amongst the older men, although it is possible that the middle-aged men were the more politically aware and less likely to admit to killings. Of particular importance was the lion hunt, traditionally a hallmark of the Maasai (*e.g.* (Spencer 1988), (Homewood & Rodgers 1991), (Kangwana 1993)) which appears to be as important culturally today as in previous decades before restrictions on hunting. Lion hunts do still account for a significant number of lions outside the park. However, there are a number of restrictions, with only the youngest age set ever carrying out lion hunts, only certain areas hunted and only during the wet season. Most importantly, all hunts, and all predator killings that were described, are carried out using traditional weapons (spears and bows and arrows). For killings by older, non-*murran*, use of traditional weapons was likely due to lack of alternatives as only two Maasai were found in Loliondo who owned guns. The increasing availability of guns from northern Kenya (Monbiot 1994) could therefore have worrying implications for the capability of Maasai to persecute large carnivores. However, the concept of bravery was so central to the *murran* lion hunt that it is hard to imagine guns ever becoming part of it. Although lion hunting has been carried out by the Maasai throughout the history of conservation in the region, lion status in the Serengeti ecosystem appears secure ((Schaller 1972b), (Chapter 4, this thesis). It has been claimed that lion hunts are increasing amongst the Maasai (Packer, *pers. comm.*). This study found no evidence for this. Indeed, numbers of hunts appeared relatively constant for several decades which, given the rapid growth rate of the Maasai population (Homewood & Rodgers 1991) indicates the frequency of hunts per person has declined. This would be expected now that school is compulsory for most boys and men of *murran* age. The incompatibility of current schooling practices and traditional Maasai practices has already been noted (Parkipuny & Berger 1993) and was also demonstrated by the Loliondo translator who had been a proper *murran* for only two years due to the demands of school, during which he saw only one lion hunt.

Implications for cheetah conservation

Initial signs were that cheetahs would benefit from Maasai behaviour towards lions and hyaenas. When examining attitudes, cheetahs were not classed in the same group as the larger predators, had a much lower salience score and were not rated as highly as problem species. Furthermore, accounts of interactions were less frequent relative to lions and hyaenas. However, much of the reason for this appeared to be confusion over the identification of cheetahs as distinct from leopards, a major predator of livestock and threat to human life. When naming photographs of each species, relatively few respondents could distinguish between leopards and cheetahs and those that could gave a very wide variety of names for the cheetah, indicating that its status as a distinct animal from leopards in Maasai perceptions was not very strong. Subsequent data collected on frequency of cheetah attacks after the difference in species was clarified indicated that there was some justification for expecting persecution to be concentrated on the larger carnivores, since there were relatively few reports of cheetah attacks on livestock and none of attacks on humans, supporting previous evidence that the cheetah is a minor pest compared to the larger species (Mizutani 1993), (Marker-Kraus 1997), (Frank 1998). Therefore, a simple solution for cheetah conservation may be to implement an education programme to raise awareness of cheetahs. The effectiveness of such a technique might be illustrated by the surprising results shown for wild dogs. Although included as a control animal initially, answers revealed that there was in fact a substantial wild dog presence outside the park. This has often been suggested *e.g.* (Creel 1996), (Mills & Gorman 1997) since wild dogs are thought to suffer the same problems with lions and hyaenas as cheetahs (Woodroffe *et al.* 1997). The results from Loliondo gave very strong evidence that wild dogs were surviving outside the park despite disappearing from the park a decade ago *e.g.* (Burrows *et al.* 1994), (Ginsberg *et al.* 1995). The results showed recognition of wild dogs was higher than for cheetahs, it was not classed as a similar species to the large predators, sightings were made relatively frequently and descriptions given were frequently very accurate on their distinct social, hunting and denning behaviour (Estes 1991). However, almost no accounts were given of wild dogs attacking livestock or people and several respondents added that attacks were unheard of. In addition, they were rated very low on the problem rating and very few people claimed to have ever killed one. This is in contrast to the reactions wild dogs and other dog-like species can raise in humans in other areas where they frequently attract a disproportionate amount of blame for livestock predation (Rasmussen 1999). It also contrasts with the data from Ngorongoro where wild dogs have not been sighted regularly for several years. Although several respondents did record having seen them, sightings were far less frequent, the descriptions far less accurate and more people associated them with threats to livestock and threats to people. At present, there is little reason to distinguish between the spotted cats. The threat from leopards is high therefore it is probably safer to assume all spotted cats are leopards unless you have a particular interest in them. If the cheetah status could be raised in the minds of the Maasai to that of the wild dog in Loliondo it could make very important contributions to the potential of the Maasai buffer zones as refuges for cheetah conservation. This could also have implications for the smaller cats and genets too. For example, servals were also classed as leopards by many of the respondents and during one trip I was shown the skin of what I was told was a young leopard but in fact turned out to be a serval.

Differences between Loliondo and Ngorongoro

One of the other interesting aspects that came out of the surveys was the differences between Loliondo and Ngorongoro. Frequently, attitudes were more negative in Ngorongoro, with respondents recording problem ratings for almost all species higher than Loliondo respondents, individual species described more frequently in terms of livestock predation and threats to human life and often classing species such as rhinoceros and hippopotamus as problem species, despite the chances of an interaction being fairly low. Furthermore, most respondents in Ngorongoro said wildlife was bad. This was in direct contrast to Loliondo where most said it was good or mixed, and most people wanted to see some sort of wildlife control implemented. Differences in the overall feelings towards wildlife were probably due to the problem with Malignant Catarrh Fever and cattle (Machange 1997), (Parkipuny 1997), (Bourn & Blench 1999) (also see Chapter 1), since most respondents in Ngorongoro reported disease as their primary reason for disliking wildlife. However, no differences were seen in attitudes towards wildebeest, the disease vector, which had similar salience and problem ratings in Loliondo and Ngorongoro. In Chapter 3 it was shown that Maasai livestock did avoid the short grass plains during the times wildebeest were, or were due to be, present. Although Loliondo Maasai were very aware of this issue and frequently cited wildebeest as a problem species for this reason, the problem actually occurs via the afterbirth and the main calving areas do not occur in Loliondo. However, disease differences do not explain why attitudes towards all species were more negative, and it could be hypothesised that the history of conflict in the NCA (see Introduction) might have had an influence on attitudes, as shown to occur both in the past and in other conflict areas *e.g.* (Western 1982).

The differences in the desire to control wildlife were also interesting. Explanations for the choices were not given sufficiently frequently to analyse statistically, but comments in Loliondo indicated that further questioning may have been appropriate since several respondents said wildlife should not be controlled overall, but that they would be happy for certain species such as leopards to be controlled. Furthermore, comments were made that suggested that it was not the word "control" that respondents reacted to but the insinuation that an external body would be involved. Several respondents said they did not want "someone" to control the wildlife because it was "their" wildlife and they would decide what to do with it. Such an issue did not appear to arise in Ngorongoro where most respondents adamantly wanted wildlife controlled but many added this was an impossible task. This contrast with Loliondo respondents might be a reflection of the far greater influence of governmental and other external groups in the NCA which, beneficial or otherwise, might serve to divorce residents from the perception of control or responsibility over their environment since most people have become accustomed to others taking decisions and action on such matters, an issue also noted in Kilimanjaro (Nelson 2000).

In contrast were the attitudes of respondents towards the protected areas. The mixed attitudes found in Loliondo, contrasting favourable attitudes to wildlife and conservation to negative attitudes towards the protected areas and authorities are found commonly in the literature *e.g.* (Infield 1988), (Fiallo & Jacobson 1995). A lack of involvement of the park authorities in the communities is a frequent contributor to such antagonism (Newmark *et al.* 1993), (Infield & Namara 2001), although occasionally the perceived managers are often not those actually responsible (Newmark *et al.* 1993). For example, most negative comments were directed towards The Tanzanian National Parks service (TANAPA) despite Game Controlled Areas being under the remit of the Wildlife Division. Interestingly, negative attitudes were similar in both Loliondo and Ngorongoro, with the primary difference occurring in the number of “no opinion”s expressed with close to half of all Loliondo respondents declining to express an opinion. In some analyses, “no opinion”s are taken to be a negative answer (*e.g.* Infield & Namara, 2001), in which case Loliondo respondents could be concluded to be mostly negative towards their local protected area. Alternatively, the lack of opinions might reflect a genuine apathy towards the park, either because they do not live close enough (although a close drive, the park boundary would have been a day’s walk from some bomas) or the park is not perceived as being connected to wildlife issues in Loliondo. In support of the latter, some respondents commented that they could not give an opinion as they had not been there. However, the most common response in Ngorongoro was the rather enigmatic reply that it allowed freedom, an unexpected choice of phrase since for all the benefits the NCA might bring, freedom is relatively restricted when compared to the neighbouring sections in Loliondo. It might be interpreted that this answer was a reflection that Maasai were happy that NCA rules allowed them to live as they wished. Alternatively, a more cynical interpretation might be that this is the answer that most felt they were meant to give.

Limitations of the study

Various limitations exist with all studies of social factors based on interviews, with one of the basic issues being whether to use structured interviews as used here or completely open approaches where no preconceived questions are asked (Randall 2001). Although this study probably would have benefited enormously from an initial period of exploratory data collection, time limitations and requirements to answer specific questions necessitated the need for a semi-structured interview. Open questions (Oppenheim 1992) (when the respondent could answer whatever he wished rather than categorise himself as a positive/negative *etc*.) were used whenever possible, although they did contribute to a vast data set.

Secondly, limitations occurred due to the difference in effort in each region. Seasonal or yearly effects on answers were assumed to be minor, allowing the one year Ngorongoro survey to be compared with Loliondo data from two years. However, the main effect of this was the lack of introductory work in Ngorongoro that was carried out in initial months in Loliondo. By getting the project known in Loliondo, a huge amount of support and goodwill was offered. However, by trying to collect data in just one year in Ngorongoro there was insufficient time to build the same relationships with various figures of authority and families which probably affected people's openness to talk. On a related matter, the influence of the politics of conservation was frequently felt, with some people answering only what they thought should be heard. In one interview in Ngorongoro, permission to continue was not granted until the local *laigwanan* was present. The *laigwanan* then proceeded to tell the respondent how to answer every question and the interview had to be excluded from the analysis. Ulterior motives for answering questions a certain way were possibly a problem in all areas throughout the study (Oppenheim 1992), (Bernard 2002), with questions on sensitive subjects such as killing protected species likely to result in biased answers. This was assumed before the survey was started and questions were initially asked about the Maasai in general rather than specific individuals to try and encourage more openness. However, it soon became apparent that most respondents were perfectly happy to talk about issues that may have been sensitive and it was felt that answers were honest enough to be used. There is even a possibility that bias swung in the opposite direction. For example, the lion hunt is a highly prestigious activity and many *laigwanan* told of how their *manyatta* was the most successful of their age group. However, most *laigwanan* made this claim, raising suspicions that some were exaggerating the number of lions killed. Bias may also have occurred in answers to livestock loss, although the lack of compensation (Parkipuny & Berger 1993) meant that exaggeration would have served no purpose other than to raise the profile of attacks. More likely was the possibility that errors were made with timing. Asking respondents how often something has occurred over a given time period is notoriously difficult for the respondent (Bernard 2002), especially if not everyone uses the western calendar (many Maasai had watches but did necessarily rely on our calendar time periods to the same extent as we do). It is highly recommended that future studies employ the revisit or diary methods used to some extent in this study.

Chapter 8: General discussion

8.1 Synthesis

In this study, various aspects of carnivore ecology have been compared from inside the Serengeti National Park in Tanzania with populations existing in two semi-protected, human inhabited buffer zones bordering the park. It has been shown that large carnivores and their prey are surviving successfully outside the core-protected area, coexisting with the pastoralist Maasai. Evidence for their success was shown first by the potential provided by prey availability outside the park, where species richness and abundance were not significantly different from levels inside the park. Instead, it was shown that prey populations could not be represented as distinct entities in each area that could be easily compared, rather that ungulates were part of a larger, highly dynamic system with both grazing areas inside and outside the park playing equally important roles at different times of the year.

Predator populations exploiting the prey availability outside the park were also shown to be highly successful outside the park, with substantial numbers shown to exist in both buffer zones. Although hyaena densities were lower in the area with lowest protection and cheetah populations appeared to be highest inside the National Park, numbers outside the park were shown to be significant additions to those in the National Park, with important implications for overall population sizes and conservation in the ecosystem. Furthermore, in contrast to previous work, no significant differences were seen between the numbers of lions recorded inside and outside the park. However, this study also showed the importance of survey technique choice when comparing carnivores in sites with differing protection regimes. Although the methods chosen in this study appeared to successful, the sightings-based methods used in many other studies showed important limitations outside the parks, indicting that previous work may have underestimated the abundance of carnivores in semi protected areas in some cases.

In addition to variation in carnivore population size, variation in certain behavioural characteristics of these populations was also investigated. It was shown that although certain behavioural adjustments were made, there were no major changes outside the park. There was some evidence for the existence of a shift in the timing of activity patterns in lions and hyaenas outside the park, but general vigilance levels of cheetahs were shown to be very similar inside and outside the park. Responses to human stimuli were also tested and although little reaction was shown inside the park, animals outside the park or with experience outside the park, showed recognition of the stimuli but displayed mixed reactions. Some showed high levels of evasion but others were apparently unconcerned.

The Maasai role in carnivore ecology was shown to be influential, but not particularly detrimental. Neither influences on carnivore prey populations through competition with livestock nor habitat alteration appeared to be major factors, however, coexistence was not represented by the romantic image of people living in harmony with their environment. Instead, Maasai attitudes towards the carnivores were generally negative and direct conflict occurred frequently, causing significant damage to human livelihoods and resulting in regular carnivore mortality. However, impacts were limited, with general attitudes towards the environment by and large positive, persecution of livestock predators limited to responses after attacks. Traditional lion hunts, although shown to still occur, were restricted by the limitations on who could attend, the seasons they were carried out and their restricted locations. Mechanisms allowing coexistence have therefore been shown by both carnivores and humans, with carnivores showing some level of avoidance behaviour and humans showing an important degree of tolerance.

There was no support for the idea that Maasai rangelands would provide valuable refuges for source cheetah populations through differential persecution of their more dangerous predators and competitors. This was firstly because large populations of their primary predators were shown to still exist outside the park. Hyaena populations in Ngorongoro and lion populations in both Ngorongoro and Loliondo were equivalent to the high densities inside the Serengeti. Secondly, Maasai in both areas showed confusion between cheetah identification and leopard identification. Since leopards were shown to be a major threat to livestock and human life, conscious differentiation in favour of cheetahs was highly unlikely. However, it is possible the Maasai rangelands may still provide considerable benefits for cheetah survival through different mechanisms. Firstly, there is some evidence for temporal separation, with lions and hyaenas outside the park appearing to be less active during the day whilst cheetahs showed continuing diurnal activity. Secondly, differential persecution may occur on a less obvious level, since cheetahs are probably less likely to be affected by the poison baits used for leopards and more difficult to kill using the traditional weapons used for lions and hyaenas.

8.2 Limitations to the scope of the study

The importance of carnivore behavioural ecology outside National Parks

The primary limitation of the study as a means of comparing the success of carnivores inside and outside the national park was the lack of data obtained on various aspects of behavioural ecology and population dynamics. To define the success of a species, population size estimates would ideally be supported by information on basic life history traits such as births, immigration, deaths and emigration. However, these parameters could not be measured in this study due to the withdrawal of permission to use radio telemetry. Such factors are particularly important for determining possible source-sink relationship between populations (Pulliam 1988), as well as determining whether the buffer zones are acting as sinks for species in the park *e.g.* (Woodroffe & Ginsberg 1998) or as sources *e.g.* (Laurenson 1995b), (Lariviere *et al*. 2000). Inability to radio collar individuals also limited a more rigorous investigation of movement patterns outside the park, such as identifying whether individuals seen in the buffer zones were residents or transients, which areas were used and whether human activity or settlements had any effect on movement patterns.

The influence of habitat differences on variation found

The second limitation with the study was the doubt over the strict comparability of the study sites. Although differences were minimised by choosing areas with similar climatic conditions and concentrating only on open grassland habitats in each study site, any comparison of locations inside and outside core-protected areas is going to be confounded to some extent by variations in the environment other than the presence or absence of people. In this study, it is suspected that the habitat matrix within which the open areas were situated and small variations in rainfall may have had some effect. The Serengeti grasslands site is in the middle of a large open area in middling rainfall conditions whilst the Loliondo and Ngorongoro sites were both located closer to wooded habitats, interspersed with areas of denser cover than grass to some degree and each was expected to be slightly wetter or drier respectively than the Serengeti site. For the purposes of this study the measures taken to ensure comparability should be sufficient, but if the study were to be improved or extended it is recommended that habitat and rainfall variation are controlled for more effectively (see "Further work", p.316).

Validity of results as a representation of human-wildlife interactions

Finally, it could be argued that this study reflected the experiences of a small section of a minority tribe in Tanzania and that the results are not applicable to either Maasai, pastoralists or humans in buffer zones in general. To some extent, this criticism may be valid, since investigation of the full extent of human-wildlife interactions in semi-protected areas would require a far larger scale study than was possible here. Sampling a scientifically significant proportion of the total population was impossible given the time constraints. Consequently, attitudes and opinions of women and children were unfortunately completely absent from the study, despite the likelihood that they would have had different views from the men interviewed (*e.g.* see (Kangwana 1993), (Gillingham 1998), (Hill 1998), (Mehta & Kellert 1998) for examples of female attitudes which tend to be more negative than men). Furthermore, attitudes and impacts are likely to be completely different for people following lifestyles that differ from the specific form of agro-pastoralism practiced by the Maasai *e.g.* (Newmark *et al*. 1993), (Newmark *et al*. 1994). However, the results found in this study are still highly applicable for understanding human-wildlife coexistence in buffer zones elsewhere for several reasons. Firstly, because the results should still be a good representation of Maasai living in Ngorongoro and Loliondo, despite not necessarily sampling a fully representative fraction of the total population that live there. This is because questionnaires were aimed at men with whom most of the major decisions that may govern Maasai impact on wildlife currently lie. Secondly, attitude surveys generally require far smaller sample sizes than most other surveys (Oppenheim 1992). Certainly the general homogeneity of results presented here within each region suggest that the attitudes sampled give a fairly accurate representation of the true general attitudes. Thirdly, transhumant, rural pastoralists are still an extremely important group in Africa, and many other parts of the world, with approximately 100,000 km^2 of land used by Maasai alone, 25% of the earths surface constituted by savannah and grassland (Fritz & Duncan 1994) and pastoralism of some form being the predominant land use on approximately one eighth of the earth’s surface (Lamprey 1983).

8.3 Relevance to existing literature

Role of semi-protected land as wildlife habitats

Much of the published literature now recognises the importance of semi-protected land as wildlife habitats *e.g.* (Wells & Brandon 1993), (Shafer 1999), (Caro 1999d) but usually add that little science is carried out in buffer zones and almost nothing is known about the biological processes that occur there. It has been stated that "the best way to stop the domino effect of species loss is to work out the principles and methods of human-wildlife cohabitation" and to do this the following are required:

1. Numerical distribution
2. Absolute / relative abundance
3. Ecological links between inside and outside
4. Reasons for differences
5. Anticipated impact on wildlife of social / land use change (Western 1989)

This study has attempted to address questions in all of these areas except no.3 (see “Limitations to the scope of the study” p.310) and in most cases offers a more optimistic view than much of the published literature. For example, the assessment of herbivore abundance in semi-protected areas provided contrasting results to those that show herbivores are less successful in the presence of people (Watson 1969), (Prins 1992), (Verlinden 1997) and supported studies that show a reduced effect of pastoralism on herbivores (Fritz & Duncan 1994), (Homewood 1994), (Machange 1997). Similarly, the study of carnivore abundance also contrasted with results from some of the more pessimistic accounts of coexistence elsewhere *e.g.* (Newmark *et al*. 1994), (Woodroffe & Ginsberg 1998), (Woodroffe 2000), (Parks *et al*. 2002), and supported previous studies that suggest coexistence can occur under certain conditions *e.g.* (Linnell *et al*. 2001). One of the primary candidates for the reason for differences between the protected and buffer zones and the impact of land use change were then investigated by studying the role of the Maasai as discussed in the following section.

The role of pastoralists and Maasai in their environment

In the past, most published literature suggested or assumed pastoralism had severe negative effects on the environment (*e.g.* (Brown 1971), (Lamprey 1983), (Sinclair & Fryxell 1985), (Prins 1992)) and several authors still maintain the importance of pastoralist effects on the environment through overgrazing *e.g.* (Du Toit & Cumming 1999), (Cowling 2000), (Illius & O'Connor 2000). In general, this study challenges many of these results and supports the increasing body of literature which argues that pastoralists (Sandford 1982), (Ellis & Swift 1988), (McCabe 1990), (Behnke & Scoones 1993), (Warren 1995), (Baars *et al*. 1997), (Charnley 1997), and specifically the Maasai (Homewood & Rodgers 1987), (Homewood & Rodgers 1991), (Parkipuny 1997), (Nelson 2000) do not have as detrimental impacts on their environment as first thought. Indeed, this thesis goes further and suggests that there may be several effects of Maasai on their environment that are beneficial for the medium sized carnivores such as cheetahs and Maasai. In previous literature it has been complained that there is no link between scientific research and the Maasai (Parkipuny & Berger 1993). It is hoped that by treating the Maasai as just another species within the ecosystem this study has managed to identify some of the key behavioural characteristics that show Maasai can coexist with wildlife extremely successfully.

8.4 Applications

The importance of semi-protected landscapes in Tanzania

Research into human-wildlife interactions outside the protection of National Parks could be extremely valuable for conservation in general. With humans occupying 95% of the earth’s surface, and just 2.8% of land set aside as nature reserves (Western 1989) for over 10 million species (Wilson 1992), the importance of the areas outside nature reserves and an understanding of the relationship between the people and species that inhabit them cannot be overestimated. This importance is further raised in Tanzania at present due to proposed land law changes, which would re-classify land into three types:

1. Protected (including National Parks, Game Reserves etc.)
2. Village lands (including residential and farm land)
3. Communal land

As part of these changes, it has been proposed that Game Controlled Areas be converted into Wildlife Management Areas, whereby management of the wildlife and area can be devolved to the local villages (Frankfurt Zoological Society and The Serengeti Regional Conservation Project 1999). Land use changes, both to proposed WMAs and for other reasons are consequently on the increase. For example, in one division of Tanzania 79% of the land is now under application for alienation (Bourn & Blench 1999). Therefore, there is currently an increased interest in the wildlife inhabiting Game Controlled Areas and the data required to make sensible management decisions.

The Maasai as conservators of Maasailand – coexistence with carnivores

The concept of various human cultures acting as natural conservationists has been studied in many areas (*e.g.* (Alvard 1993), (Alvard 1998), (Low 1996) including the potential of pastoralists as conservationists (Ruttan & Mulder 1999), (Borgerhoff Mulder & Ruttan 2000). In most cases, conservation is not shown to be an adaptive strategy (Alvard 1998), (but see (Ruttan & Mulder 1999)). However, it can occur as a consequence of incidental actions. In the case of the Maasai, it appears conservation results are achieved as a by-product of their reliance on pastoralism and partly due to low population density or lack of technology (Low 1996), rather than as an adaptation to their environment or a specified goal (although attitudes towards conservation were shown to be positive in Chapter 7). However, whatever the mechanisms, the Maasai appear to be highly compatible with conservation and the potential role for Maasai in the developing field of community conservation is high. In one study, Heinen (Heinen 1996) attempted to classify the factors that lead to favourable or unfavourable conditions for wildlife and humans to live successfully in the same area. Key factors identified included relatively homogenous societies with local controls to exclude those who may cheat the system, together with economic incentives for conservation through resource extraction, tourism and buffer zone management. The Maasai in the Serengeti ecosystem exhibit all of these factors. They exist as a remarkably homogenous society with a relatively narrow spectrum of interests, in contrast to areas where human diversity is one of the key problems for implementing community conservation schemes (Gillingham 1998). Although not immediately obvious (Ostrom *et al.* 1999), a system for managing another apparent common property resource, the grazing lands, is already in place. Homogeneity also serves to exclude cheaters, with evidence of how outside interests can be thwarted when required. An example of this is provided by the Maasai of Amboseli who, after being persuaded of the advantages of conservation, were very effective at stopping poachers from outside the community (Western 1994), (Lindsay 1987). Although, bearing in mind the identification problems in of chapter 7, clarification of the difference between cheaters and cheetahs may have to be established first! In addition, the most popular tourist destinations in Tanzania are on their doorstep, with Ngorongoro the most visited tourist attraction in Tanzania, attracting 25% of all tourists (Homewood & Rodgers 1991). Finally, this study shows that the Maasai attitudes are very favourable for conservation on the whole and they even have the potential for promoting conservation of some species, with wild dogs apparently surviving better on Maasai lands, cheetahs possibly benefiting (or, following an education programme, very likely benefiting) and very tentative evidence that striped hyaenas may even benefit. Although this potential for Maasailand has already been recognised *e.g.* (Western 1994), (Nelson 2000) there is little sign of application in many Maasai areas, or indeed in any other pastoralist buffer zones *e.g.* (Turner 1999).

Manipulation of buffer zones to promote successful coexistence

Finally, one of the aims of this study was to understand better the factors that could lead to coexistence between humans and wildlife in order that these factors could be manipulated in other areas to encourage coexistence. Therefore this study ends by proposing that pastoralists are encouraged to live in buffer zones to National Parks as one of the land uses that is most compatible to the conservation activities of the core. This could possibly be carried out through beneficial taxing schemes whereby the cheapest way to live in buffer zones would be to conduct pastoralism. However, such measures would have to be carried out in conjunction with recognition of the traditional methods of transhumant pastoralism rather than commercial ranching. Furthermore, such action would need to be carried out soon. With increasing political and economic pressures to convert land uses and lack of compensation for the consequences of coexistence with wildlife, there is a strong potential that the current positive situation for conservation in areas like Loliondo might not be stable in the long-term. One of the main pressures influencing those already in buffer zones is the option for large-scale conversion to agriculture. For example, Norton-Griffiths (Norton-Griffiths 1995) calculated the potential income from various land use options for residents of buffer zones around the Masai Mara Game Reserve and found that profits to the landowners of the land varied from 1.9% of total tourist revenues to just over 5% of land leased to commercial farmers. In contrast, it was calculated that profits 23 times higher could be obtained if landowners used their land for cash crops. Consequently, current trends for various areas of Maasailand, especially in Kenya, but increasingly in Tanzania (Norton-Griffiths 1995), are for large-scale change, by either Maasai or others moving Maasai out. Three such ranches adjacent to the Masai Mara have shown an increase in agricultural land of 3% to 12% in 21 years (Sitati, 1997) whilst in Tanzania the *ujamaa* process has facilitated the influx of agriculture (Homewood 1995). As a result it is vital to recognise the positive aspects of pastoralism compared with the negative aspects suffered by people when coexisting with wildlife, especially taxa such as carnivores that have such a high conservation value but high cost of coexistence.

8.5 Further work

By attempting to cover a subject as broad as human-wildlife interactions, the future study possibilities are almost endless. However, there are a number of key areas highlighted by this study, in particular following the limitations described on p.306 but also for broadening beyond Maasai-wildlife issues that should be explored:

1. One of the primary limitations of the project was the comparability of the study sites. Although this was controlled to some degree by only comparing open grassland sites in each region, each site may still have been affected by the variations in grass species, soil type, surrounding habitat matrix and rainfall. If this research was extended it should therefore be expanded to compare several habitat types in the park and several outside the park to try and quantify and control for all the different environmental and abiotic influences on each site. Furthermore, many other factors that could have been influential to analyses in this thesis were not included, such as distances to the nearest human habitation, to roads or to the park boundary. Incorporation of all of these variables could be carried out with an extended survey across other habitats, using a GIS to pool data from satellite imagery, aerial photographs and ground-truthing to re-analyse call-ins and line transects. Much of these data already exist and therefore this is one possible extension that is immediately viable.

2. A more radical alternative to attempting to control for habitat differences would be to attempt a manipulation study. One of the limitations of research involving people is that the restrictions on manipulation are much tighter, because people's lives cannot be experimented with, forcing "natural experiments" where roughly experimental conditions exist. For example, (Homewood *et al*. 2001) exploited the international and protected area boundaries in the north of the Serengeti to create a natural 4-way experiment to compare the effects of land use policy and political environment on wildlife abundance trends. However, natural experiments necessarily involve many other factors that need to be controlled for. To really investigate the effects and relationships between humans and their environment properly manipulation experiments need to be carried out, for example allowing people back into a National Park in some areas for comparison with areas where exclusion is maintained, or when protected areas are newly gazetted the restrictions placed on human habitants should be introduced in a controlled manner in experimental areas to determine the actual effects of policies.
3. Most of this thesis was concerned with carnivores. However, the success of ungulates and other taxa in semi-protected areas have also been neglected whilst evidence from this study suggests that ungulate success in semi-protected areas can be very high. Further studies of ungulates outside parks could include comparisons of behaviour; analysing whether group sizes, structures and even species composition vary outside the park; examining spatial relationships with livestock; examining whether coexistence occurs at a local level (for example herbivores may exploit some areas more at night when humans and livestock are not present) or at a larger scale (for example variation in seasonal use of rangelands by wildebeest and cattle in Ngorongoro). Equally, studies could be made of conflict with humans, looking at the potential for crop raiding which would presumably be a more important factor to the west of the Serengeti.
4. Further work that would benefit this immediate study in particular would be an extension of the comparisons of the carnivore populations inside and outside the park. Firstly, due to limitations of time and space, population structures inside and outside the park were not compared, although the preliminary data showed some interesting results such as the strong presence of adult male lions outside the park in direct contrast to previous studies *e.g.* (Borner 1992) or the high number of breeding female cheetahs in Loliondo. Secondly, comparisons of behavioural

ecology should have been made in far greater depth. One of the key variables not measured in this study was cheetah reproductive success, despite this being the key limiting factor inside the park. As a result, the true potential of the population outside the park to act as a "source" population could only be estimated. This limitation was unfortunately imposed due to restrictions on the use of radio telemetry outside the parks, which meant cheetahs could not be regularly relocated to measure cub survival (Laurenson 1994). Radio telemetry could have opened up a whole range of behavioural studies that could be vital in fully understanding the coexistence of carnivores and humans, including monitoring ranging patterns, measuring association or avoidance of human settlements or roads and investigating detailed behavioural patterns such as temporal avoidance of humans.

5. Further work could also be carried out on the behavioural work presented in this thesis since these data did not give a firm picture of variation in behaviour outside the park. Diurnal activity should be measured continuously for a number of different predators to determine whether temporal shifts are occurring, behavioural studies of cheetahs should be extended to hunting behaviour, examining behaviour after kills in particular, and playback data should be analysed using different cut-off times to measure responses (*e.g.* comparing behaviour before the playback with the first five minutes afterwards rather than thirty).
6. Finally, future research involving cultures other than pastoralism should be explored. Although pastoralism is a major form of lifestyle, especially in Sub-Saharan Africa, it is also vital to understand how subsistence hunting lifestyles, agricultural lifestyles and even urban lifestyles co-exist with different species, if at all, and to understand the mechanisms through which coexistence occurs. A possible natural experiment along these lines already exists in the Serengeti ecosystem, with the National Park acting as the control and agricultural communities inhabiting western buffer zones, pastoralists to the east and subsistence hunters to the southeast.

With such a disproportionate amount of research carried out in core-protected areas this study attempts to redress this balance to some degree. I finish this section with a call for future research to avoid the lure of the habituated study species and beautiful scenery in National Parks and start to investigate ecological relationships in truly natural environments – those that are not actively managed to exclude people.

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Chapter 10: Appendices

10.1 Appendix I – Variables recorded when sighting predators

Cheetah sightings

Reference details

Sighting / Reference number - each sighting had a unique reference number. This number was then used when recording all other data at the sighting, providing a link to everything recorded at a sighting. This removed the need to re-record basic details on the cheetah or location before data on hunts, kills etc. are taken. Every cheetah was also identified by its first sighting number.

Date / Time - the date and time of day seen was recorded to show seasonal and daily variation in sightings.

Photography - The film number and individual photograph number was recorded for any photographs taken.

Locational details

Grid reference - the exact location of every sighting was recorded from a Global Positioning System (GPS)

Habitat - Habitat was determined simply as open grassland, woodland, savannah or riverine.

Exact location - the exact location within the habitat was also noted, for example under a bush or walking through long, medium or short grass.

Study site - Whether the sighting was made in the LGCA, NCA or Serengeti

Area - The area within the study site where the sighting was made was also recorded.

Cheetah details

Cheetah identity - cheetahs have unique spot patterns (Bertram, 1978), (Caro and Durant, 1992) and therefore they can be individually recognised. Previously recorded cheetahs were therefore recognised by comparison with a existing ‘photos. New sightings were named by their sighting number.

Composition - the ages, sexes and total number of cheetahs sighted in the group, including young, was recorded. Juvenile ageing is based upon an ageing chart produced by previous project workers (Caro, 1994), (Frame, unpublished).

Belly size - belly size was measured on a 5 point scale, with 1 being starving and 5 looking like a basketball had been swallowed. Hunting usually occurred when belly size had reached 3. Depending on the size before eating, animals that had just eaten were usually 4-5.

Tameness - tameness was recorded on a scale of 0-5. This was also a useful identification aid, especially of shy individuals.

Approach distance	Score
Can approach within 15m	0
Moved off by 15m	1
Moved off by 30m	2
Moved off at 50m	3
Crouched until observer close, then ran	4
Ran off at 500-1000m	5

Sighting circumstances

Weather - weather was recorded as sunny (S) if the sun is uncovered by cloud, low cloud cover (LC) if the sun was partially obscured, medium cloud cover (MC) if the sun was fully obscured, high cloud cover (HC) if the whole sky was heavily clouded, light rain or drizzle (LR), heavy rain (HR) or fog (FG).

How - how the sighting was made was recorded *e.g.* from driving, from a scanning point (the number of which was recorded), from other researchers *etc.*

Distance - the distance from which the cheetah was sighted in metres was recorded.

Direction - the compass direction toward the sighting was recorded.

Activity - the activity of the cheetah when sighted was recorded.

Other predator sightings

As with cheetahs, whenever another carnivore species is seen it is recorded. This is primarily for lions and hyaenas. However, all carnivores larger than a mongoose are being noted. Data recorded are summarised in Table 97.

Table 97 - Predator details recorded

Data	Notes
Date / time	
Area	Loliondo / Serengeti, including area.
Species	
Number	Number in group
Composition	Sexes, ages
Identification	For lions if relevant.
Habitat	As cheetah definitions
GPS	UTM grid reference
Activity	As for cheetahs except to distinction was made between different forms of lying down
Belly size	Based on same scale used for cheetahs after discussion with lion researchers (Whitman, pers. comm.)
Photographs	References to photos taken

10.2 Appendix II – Summary of all species seen during transect surveys

Table 98 – Summary of all species sighted on line, strip and point transects in each habitat stratum ((G)rass, (S)avanna, (T)hicket) of each study area. Sightings are described as number of individuals (Ind.), group sightings (Gps.) and individuals per transect (Ind./T). Species in bold had sufficient sightings for Distance analysis.

		Loliondo						Ngorongoro							Serengeti			Total
Transect		Line			Str	Point		Line			Strip		Point		Line	Str	Pt.	All
Habitat		G	S	W	G	G	S	G	S	W	G	S	G	S	G	G	G	
Baboon	Ind.	0	1	26	0	50	0	8	5	0	0	0	0	0	7	0	0	97
	Gps	0	1	3	0	2	0	1	1	0	0	0	0	0	1	0	0	9
	Ind./T	0.0	0.0	0.5	0.0	0.2	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Bat-eared fox	Ind.	0	0	0	0	0	0	4	0	0	0	0	0	0	13	0	4	21
	Gps	0	0	0	0	0	0	1	0	0	0	0	0	0	6	0	2	9
	Ind./T	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Buffalo	Ind.	0	0	0	0	38	0	70	0	0	0	0	87	0	5	0	308	508
	Gps	0	0	0	0	1	0	1	0	0	0	0	4	0	1	0	6	13
	Ind./T	0.0	0.0	0.0	0.0	0.1	0.0	0.9	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.6	0.3
Cattle	Ind.	8804	11364	2791	763	18589	1602	314	977	505	0	0	322	0	0	0	0	46031
	Gps	66	117	49	6	135	13	10	12	3	0	0	5	0	0	0	0	416
	Ind./T	108.7	164.7	49.8	76.3	62.4	59.3	4.2	42.5	36.1	0.0	0.0	2.2	0.0	0.0	0.0	0.0	29.2
Cheetah	Ind.	3	1	4	1	8	5	3	2	0	0	0	0	0	8	0	21	56
	Gps	1	1	1	1	4	1	2	1	0	0	0	0	0	4	0	15	31
	Ind./T	0.0	0.0	0.1	0.1	0.0	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dik-dik	Ind.	2	6	15	0	0	0	0	2	8	0	1	0	0	0	0	0	34
	Gps	1	3	11	0	0	0	0	1	5	0	1	0	0	0	0	0	22
	Ind./T	0.0	0.1	0.3	0.0	0.0	0.0	0.0	0.1	0.6	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Dog	Ind.	4	3	0	0	2	0	0	0	0	0	0	5	0	0	0	0	14
	Gps	3	3	0	0	2	0	0	0	0	0	0	3	0	0	0	0	11
	Ind./T	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Duiker	Ind.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	Gps	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	Ind./T	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eland	Ind.	215	43	30	5	478	33	565	23	0	404	0	1482	0	257	22	354	3911
	Gps	17	4	4	2	30	3	15	2	0	12	0	41	0	12	1	33	176
	Ind./T	2.7	0.6	0.5	0.5	1.6	1.2	7.5	1.0	0.0	14.4	0.0	10.2	0.0	1.2	4.4	0.7	2.5
Elephant	Ind.	0	0	15	0	0	10	0	0	1	0	13	0	0	140	0	178	357
	Gps	0	0	1	0	0	1	0	0	1	0	2	0	0	9	0	15	29
	Ind./T	0.0	0.0	0.3	0.0	0.0	0.4	0.0	0.0	0.1	0.0	3.3	0.0	0.0	0.7	0.0	0.3	0.2
Giraffe	Ind.	205	109	75	0	345	29	32	137	31	1	3	23	3	24	0	65	1082
	Gps	22	19	16	0	57	6	9	12	10	1	1	15	1	8	0	29	206

		Loliondo						Ngorongoro							Serengeti			Total
	Ind./T	2.5	1.6	1.3	0.0	1.2	1.1	0.4	6.0	2.2	0.0	0.8	0.2	0.5	0.1	0.0	0.1	0.7
Grant's gazelle	Ind.	4126	891	382	464	7588	814	9146	549	68	759	83	5330	2	7390	335	11609	49536
	Gps	271	92	42	49	468	42	266	42	7	67	5	354	1	390	14	606	2716
	Ind./T	50.9	12.9	6.8	46.4	25.5	30.1	121.9	23.9	4.9	27.1	20.8	36.5	0.3	34.5	67.0	22.2	31.4
Hare	Ind.	0	0	0	1	0	0	3	1	0	0	0	1	0	3	0	0	9
	Gps	0	0	0	1	0	0	3	1	0	0	0	1	0	3	0	0	9
	Ind./T	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hyaena	Ind.	2	0	0	2	2	0	17	2	0	49	0	35	0	62	2	35	208
	Gps	2	0	0	1	1	0	10	2	0	18	0	22	0	40	1	21	118
	Ind./T	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.1	0.0	1.8	0.0	0.2	0.0	0.3	0.4	0.1	0.1
Impala	Ind.	66	584	732	75	191	25	0	18	45	0	21	0	0	0	0	0	1757
	Gps	6	49	56	1	12	2	0	3	3	0	2	0	0	0	0	0	134
	Ind./T	0.8	8.5	13.1	7.5	0.6	0.9	0.0	0.8	3.2	0.0	5.3	0.0	0.0	0.0	0.0	0.0	1.1
Jackal	Ind.	14	5	6	1	10	0	16	2	0	6	0	12	0	12	0	9	93
	Gps	11	4	3	1	7	0	12	2	0	4	0	9	0	9	0	9	71
	Ind./T	0.2	0.1	0.1	0.1	0.0	0.0	0.2	0.1	0.0	0.2	0.0	0.1	0.0	0.1	0.0	0.0	0.1
Klipspringer	Ind.	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	4
	Gps	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	Ind./T	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kongoni	Ind.	245	192	255	0	607	41	12	0	2	2	0	1	0	1229	68	2008	4662
	Gps	41	37	54	0	89	9	2	0	1	2	0	1	0	243	12	330	821
	Ind./T	3.0	2.8	4.6	0.0	2.0	1.5	0.2	0.0	0.1	0.1	0.0	0.0	0.0	5.7	13.6	3.8	3.0
Lion	Ind.	0	0	0	1	3	0	7	0	0	0	0	0	0	46	1	16	74
	Gps	0	0	0	1	2	0	1	0	0	0	0	0	0	7	1	11	23
	Ind./T	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0
Man	Ind.	82	309	124	13	136	11	37	47	4	3	1	26	0	0	0	0	793
	Gps	45	129	53	7	76	4	21	15	4	3	1	19	0	0	0	0	377
	Ind./T	1.0	4.5	2.2	1.3	0.5	0.4	0.5	2.0	0.3	0.1	0.3	0.2	0.0	0.0	0.0	0.0	0.5
Oryx	Ind.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
	Gps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	Ind./T	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ostrich	Ind.	177	78	7	55	586	28	437	33	0	71	7	312	2	190	4	477	2464
	Gps	46	19	4	13	162	13	40	8	0	12	2	77	1	78	3	189	667
	Ind./T	2.2	1.1	0.1	5.5	2.0	1.0	5.8	1.4	0.0	2.5	1.8	2.1	0.3	0.9	0.8	0.9	1.6
Reedbuck	Ind.	0	0	0	0	0	0	0	0	0	0	0	0	0	106	0	3	109
	Gps	0	0	0	0	0	0	0	0	0	0	0	0	0	22	0	1	23
	Ind./T	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.1
Serval	Ind.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
	Gps	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
	Ind./T	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sheep / goats	Ind.	95	3208	2440	388	1719	52	582	1237	10	357	233	1821	0	0	0	0	12142
	Gps	4	41	28	5	19	2	15	14	1	2	1	23	0	0	0	0	155

		Loliondo						Ngorongoro							Serengeti			Total
	Ind./T	1.2	46.5	43.6	38.8	5.8	1.9	7.8	53.8	0.7	12.8	58.3	12.5	0.0	0.0	0.0	0.0	7.7
Steinbuck	Ind.	1	4	4	0	1	1	1	4	3	0	0	0	0	0	0	0	19
	Gps	1	4	3	0	1	1	1	4	3	0	0	0	0	0	0	0	18
	Ind./T	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
T.gazelle	Ind.	10222	1456	1156	6889	9831	349	7801	341	2	11692	454	28943	5	27831	1688	42705	151365
	Gps	482	150	85	265	436	12	434	48	1	596	21	563	4	799	83	1093	5072
	Ind./T	126.2	21.1	20.6	688.9	33.0	12.9	104.0	14.8	0.1	417.6	113.5	198.2	0.8	130.1	337.6	81.8	95.9
Topi	Ind.	62	101	69	1	112	1	0	0	0	29	0	1	0	609	35	859	1879
	Gps	14	11	24	1	25	1	0	0	0	2	0	1	0	136	9	201	425
	Ind./T	0.8	1.5	1.2	0.1	0.4	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	2.8	7.0	1.6	1.2
Warthog	Ind.	15	7	11	0	8	0	0	0	0	2	0	0	0	129	6	111	289
	Gps	6	2	4	0	2	0	0	0	0	1	0	0	0	70	2	52	139
	Ind./T	0.2	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.6	1.2	0.2	0.2
Waterbuck	Ind.	0	0	1	0	0	0	0	0	0	0	0	0	0	14	0	5	20
	Gps	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	3
	Ind./T	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Wildcat	Ind.	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
	Gps	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
	Ind./T	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Wildebeest	Ind.	812	101	237	1718	4063	217	5296	2553	0	27255	2346	94582	570	6302	21	52573	198646
	Gps	60	16	11	122	172	14	23	17	0	376	19	279	3	53	4	138	1307
	Ind./T	10.0	1.5	4.2	171.8	13.6	8.0	70.6	111.0	0.0	973.4	586.5	647.8	95.0	29.4	4.2	100.7	125.9
Zebra	Ind.	5301	2882	1239	2853	14109	2746	1795	1393	2	3653	168	11331	0	10815	3102	32156	93545
	Gps	101	51	39	113	297	24	43	18	1	227	15	275	0	236	88	491	2019
	Ind./T	65.4	41.8	22.1	285.3	47.3	101.7	23.9	60.6	0.1	130.5	42.0	77.6	0.0	50.5	620.4	61.6	59.3
Total species	28							26							22			

10.3 Appendix III - Call-in response patterns

Behaviour at the call-in

Arrival times

Table 99 – Mean of earliest common carnivore arrivals

Species	Loliondo	Ngorongoro	Serengeti	All regions
Black backed jackal	16 minutes (n=70)	24 minutes (n=11)	21 minutes (n=11)	17 minutes (n=92)
Golden jackal	23 minutes (n=22)	21 minutes (n=13)	31 minutes (n=5)	23 minutes (n=40)
Spotted hyaena	13 minutes (n=91)	13 minutes (n=41)	17 minutes (n=59)	14 minutes (n=191)
Lion	31 minutes (n=28)	25 minutes (n=6)	27 minutes (n=14)	29 minutes (n=48)

Table 100 – Mean of earliest common raptor arrival times

Species	Time
White backed vulture	23 minutes (n=25)
Lappet faced vulture	24 minutes (n=25)
Tawney eagle	19 minutes (n=43)
White headed vulture	31 minutes (n=8)
Hooded vulture	28 minutes (n=27)

Distance to first sighting

Every time a species was first seen responding to a call-in the distance to the speaker was estimated, giving an indication of the area that should be observed when carrying out call-ins.

Table 101 – Mean distance (m) first sighted

Region	Black blacked jackal	Golden jackal	Hyaena	Lion
Loliondo	113.13	239.09	164.81	252.80
Ngorongoro	92.19	167.50	169.44	118.89
Serengeti	116.32	142.86	200.97	247.14
Mean	111.53	197.65	182.58	228.47

Table 102 – Mean closest approach (m) to call-ins

Region	Black blacked jackal	Golden jackal	Hyaena	Lion
Loliondo	67.00	216.97	63.57	76.48
Ngorongoro	63.75	140.44	64.37	47.59
Serengeti	55.00	129.29	91.17	77.14
Mean	65.35	174.09	76.50	71.81

Inter and intra-species interference of responses to call-ins

Responses to auditory cue

Of the species responding to call-ins, all but the kite, fish eagle, side striped jackal, pied crow, martial eagle and griffon vulture responded at least once when no other species were present, indicating that most species were capable of responding to the auditory cue alone and not only to the presence of other scavengers. Of those that were not recorded responding independently of other species, all were rare sightings and therefore no conclusions can be realistically drawn on the cues they responded to.

Effects of species already present at call-ins

It might be expected that responses would be affected by species already present at the call-in. For example, lions may be more likely to respond to call-ins with many vultures or hyaenas already present whilst hyaenas may avoid call-ins where many lions are already present. To investigate the influence species present at a call-in had on further responses from the same or different species, the number of jackals (all species pooled), spotted hyaenas, lions and raptors (all species pooled) already present were recorded every time a response to a call-in was noted. The number of each species that arrived during any given presence level of a second species was then calculated (for example, across 222.7 hours of call-in time, 61 lions arrived when no hyaenas were present, 21 arrived when 1 hyaena was present *etc.*) The number of responses that might be expected was then calculated by calculating the proportion of call-ins that was occupied by any given level of a species presence (for example, no hyaenas were present 54.1% of the time, 1 hyaena was present 11.64% of the time *etc.*). The expected value for any given level was then calculated as:

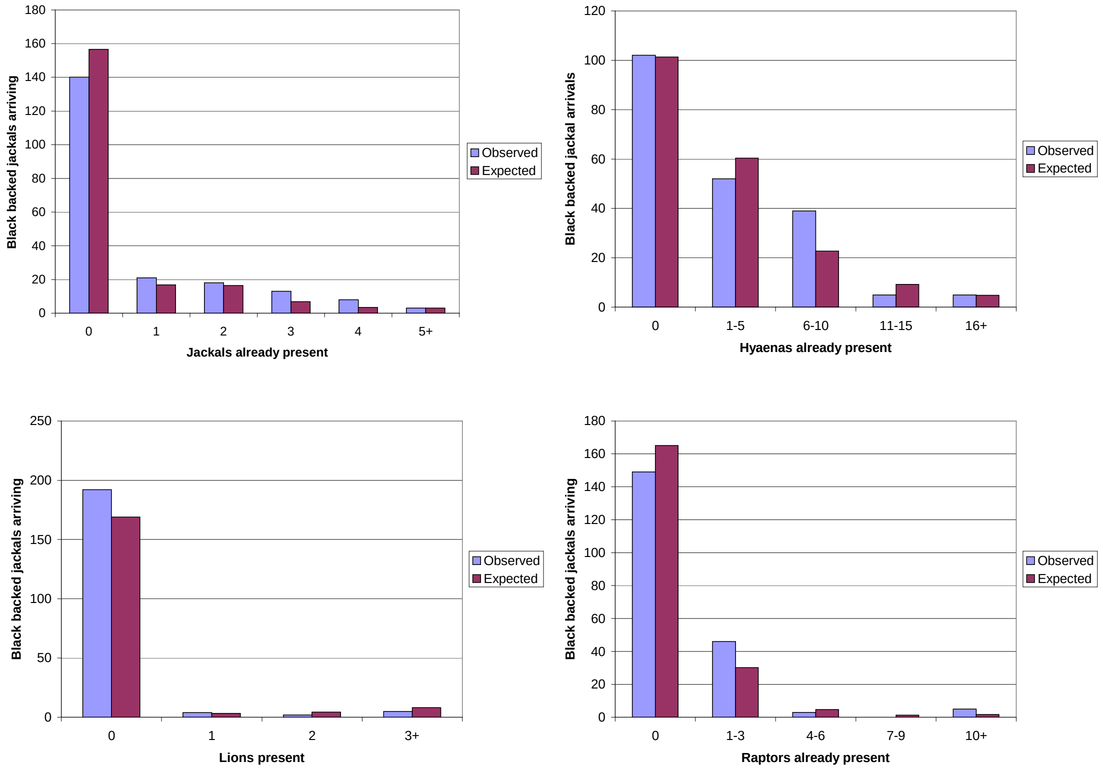
$$P \times T$$

where *P* = proportion of time spent at any given presence level and *T* = total responses for responding species. Continuing the above example, 185 lion responses were recorded during the 222.7 hours of call-ins analysed, therefore if hyaena presence had no effect on lion responses, 100 lions (0.541 x 185 = 100.09) would be expected to arrive when no hyaenas were present, 22 (0.116 x 185) when 1 hyaena was present *etc*). The observed and expected results were compared using a Chi squared test.

Black backed jackals

Black backed jackal response distribution was affected to a small degree by the presence of other species. The presence of other jackals or raptors had a small positive effect, with slightly fewer than expected responding when no other jackals or raptors were present and slightly more responding when raptors or other jackals were present (jackal presence: χ^2_5=14.9, p=0.011; raptor presence: χ^2_4=18.8, p=0.001). The presence of hyaenas caused a significant deviation from random responses (χ^2_4=14.9, p=0.005) although no obvious positive or negative effect could be determined. Lion presence did not significantly affect black backed jackal responses (χ^2_3=5.9, p=0.115).

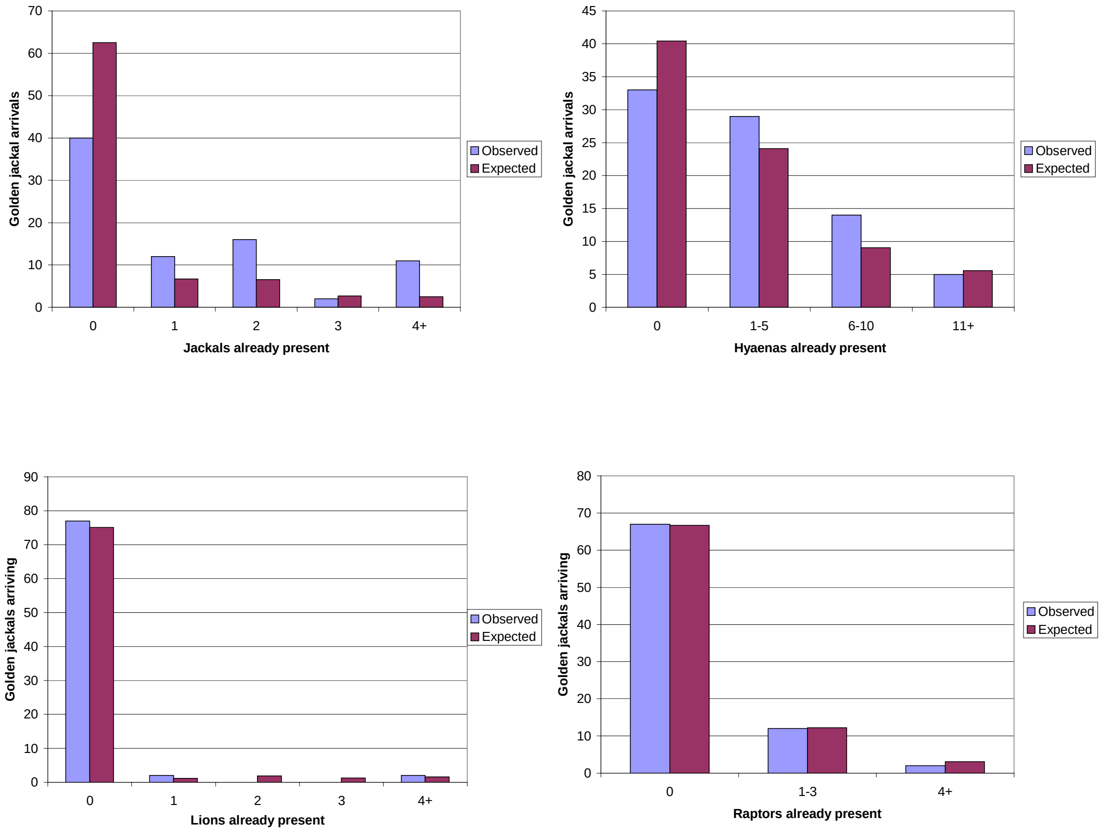
Figure 61 - Comparison of number of expected (random) and actual black backed jackal responses whilst other species are already present at the speakers. Top left=jackals, Top right=Hyaenas, Bottom left=Other lions, Bottom right=Raptors



Golden jackals

The golden jackal response distribution was only affected by the presence of other jackals, with significantly fewer than expected responding when no other jackals were already present and more than expected when jackals were already present ($\chi^2_4=54.1$, $p<0.001$). Responses also appeared to be positively influenced by hyaena presence, although the difference from random was insignificant ($\chi^2_3=5.1$, $p=0.162$) but were irrespective of the presence of lions ($\chi^2_4=4.0$, $p=0.406$) or raptors ($\chi^2_2=3.9$, $p=0.823$).

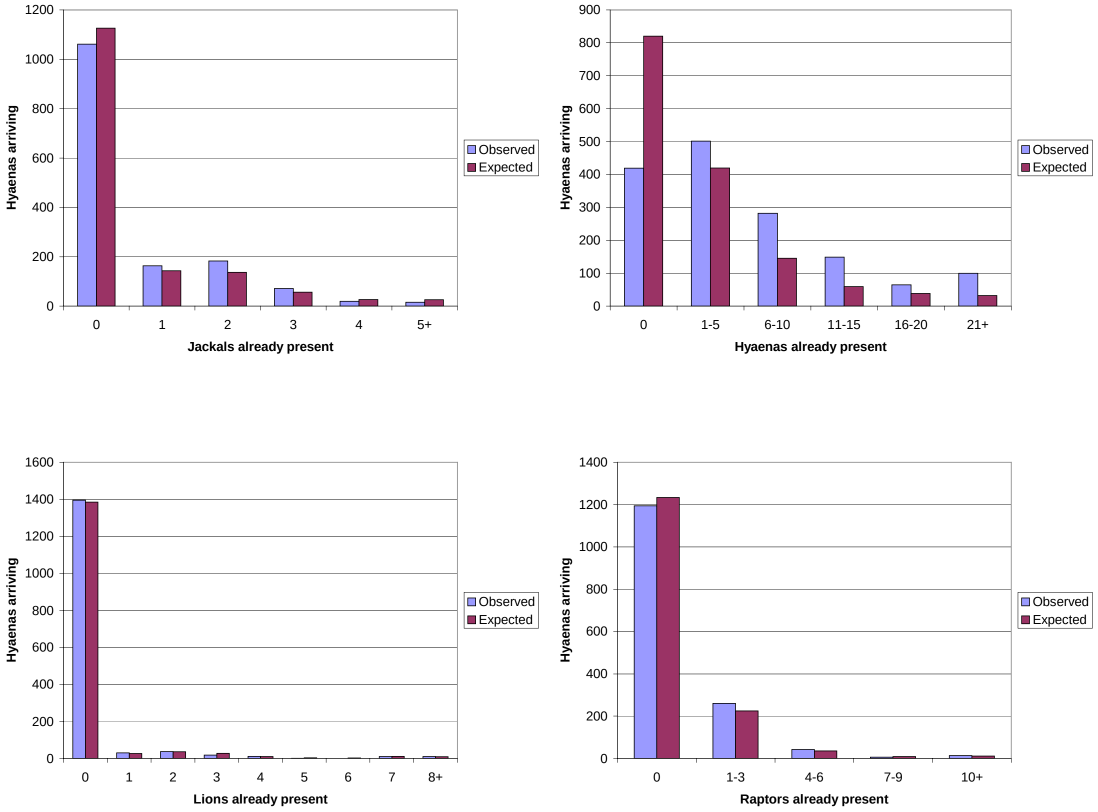
Figure 62- Comparison of number of expected (random) and actual golden jackal responses whilst other species are already present at the speakers. Top left=jackals, Top right=Hyaenas, Bottom left=Other lions, Bottom right=Raptors



Hyaenas

Hyaena responses were affected positively by the presence of other hyaenas (χ^2_5=630.6, p<0.001) and jackals (χ^2_5=31.6, p<0.001) and slightly positively by the presence of raptors (χ^2_4=9.4, p=0.052). Lion presence did not appear to affect hyaena response (χ^2_8=9.5, p=0.302).

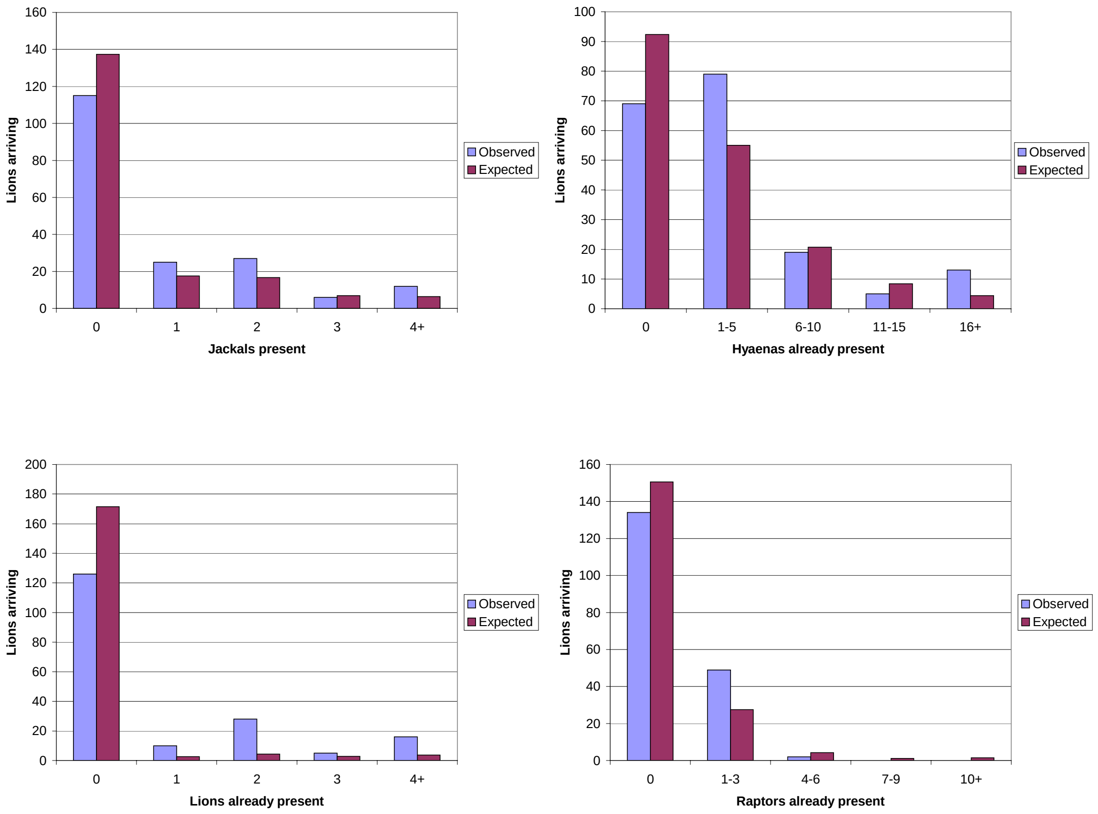
Figure 63- Comparison of number of expected (random) and actual spotted hyaena responses whilst other species are already present at the speakers. Top left=jackals, Top right=Hyaenas, Bottom left=Other lions, Bottom right=Raptors



Lions

Lion responses appeared to be more likely than random whenever another species was already at the speaker, showing response distributions significantly different from random whichever species was already present. In all cases responses were lower than expected when no other individuals had responded and higher than expected when animals were already at the speaker. The strongest effect was shown by the presence of other lions (χ^2_4=205.1, p<0.001), but also hyaenas (χ^2_4=34.3, p<0.001), , raptors (χ^2_4=22.5, p<0.001) and jackals (χ^2_4=18.1, p=0.001).

Figure 64- Comparison of number of expected (random) and actual lion responses whilst other species are already present at the speakers. Top left=jackals, Top right=Hyaenas, Bottom left=Other lions, Bottom right=Raptors



Effect of carnivore presence on raptor responses

The effect of carnivore presence on raptor responses was tested for the three most common vulture species respondents and the two most common eagle respondents. Responses for all of the vulture species were significantly different from random with respect to the presence of jackals, hyaenas or other raptors and in every case the effect was positive with more birds than expected arriving when other species were already at the speaker. The one exception was the response of lappet-faced vultures which responded close to randomly with respect to hyaena presence. However, none of the bird species appeared to be affected by lion presence. The eagles responded more or less irrespective of the species already present, although bataleurs tended to respond more commonly than expected when hyaenas were present whilst Tawney eagles were slightly more common when other raptors were present (see Table).

Table 103 – Effect of carnivore presence on various raptor species. Significant results indicate responses do not follow a random pattern with respect to the species already present.

	Bataleurs (n=8)			Hooded vultures (n=76)			Lappet faced vultures (n=52)			Tawney Eagles (n=55)			White backed vultures (n=105)		
Species present	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P
Jackals	2	0.5	0.769	5	36.1	<0.000	4	35.8	<0.000	4	6.1	0.194	5	28.7	<0.000
Hyaenas	2	8.4	0.015	4	32.5	<0.000	5	11.8	0.038	3	4.2	0.241	5	40.2	<0.000
Lions	NA	NA	NA	4	2.2	0.705	4	5.2	0.269	4	4.4	0.359	4	12.8	0.012
Raptors	2	0.4	0.832	3	82.3	<0.000	2	49.6	<0.000	3	7.0	0.071	3	649.2	<0.000

Table 104 – Estimates of area sampled (km^2) during call-in surveys (based on estimated average audible areas per call-in)

Survey	Loliondo		Ngorongoro		Serengeti		Total	
	Lions	Hyaenas	Lions	Hyaenas	Lions	Hyaenas	Lions	Hyaenas
1	53	71	0	0	0	0	53	71
2	187	247	0	0	134	177	320	424
3	200	266	0	0	134	177	334	442
4	134	177	0	0	134	177	267	353
5	147	194	160.	212	134	177	441	583
6	227	300	160.	212	134	177	521	689
7	200	265	147	194	134	177	481	636
8	240	318	160.	212	134	177	534	707
Total	1388	1838	627.	830	935	1237	2950	3905

10.4 Appendix IV - Analysis of carnivore diversity

Carnivore species richness was compared by looking at all species recorded by any method in each of the three study sites (for details of methods, see appropriate sections). The results were compared to the species list for carnivores larger than a mongoose recorded as present in the Serengeti-Mara ecosystem (Sinclair & Arcese 1995). Since the study was not designed to be a comprehensive survey of all carnivore species, some species were more or less likely to be seen. For example, nocturnal species were unlikely to be seen outside the park where no nocturnal work was carried out. However, since the project was based within the National Park, nocturnal species were occasionally recorded during late returns to the house. Species not deemed to have an equal chance of sighting in all study areas are marked in the results and were excluded from the analysis.

Table 105 – Carnivore species listed as present in the Serengeti-Mara ecosystem and their recorded presence during this study. The codes refer to the methods that revealed the species presence: (C=Call-in , P=Personal sighting, S=Maasai survey, T=transect, X=no evidence). Totals are given for all species likely to have been seen during the survey, and all species including more nocturnal or habitat specific species marked with an asterix that were unlikely to be spotted outside the park, even if present.

Common name	Latin name	Loliondo	Ngorongoro	Serengeti
Aardwolf	*Proteles cristatus*	X	X	P
African civet*	*Viverra civetta*	X	X	P
African wildcat	*Felis sylvestris*	X	P,T	P
Bat-eared fox	*Otocyon megalotis*	P	P,T	P,T
Black backed jackal	*Canis mesomelas*	C,P,T	C,P,S,T	C,P,T
Caracal	*Felis caracal*	X	P	P
Cheetah	*Acinonyx jubatus*	P,S,T	P,S,T	P,T
Common genet	*Genetta genetta*	X	P	P
Golden jackal	*Canis aureus*	C,P,S,T	C,P,S,T	C,P,T
Honey badger*	*Melivora capensis*	X	P	P
Leopard*	*Panthera pardus*	S	S	P
Lion	*Panthera leo*	C,P,S,T	C,P,S,T	C,P,T
Palm civet*	*Nandinia binotata*	X	X	X
Serval	*Felis serval*	S	P	P,T

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* Unlikely to be seen outside park as fewer nocturnal journeys were made

Common name	Latin name	Loliondo	Ngorongoro	Serengeti
Side striped jackal	*Canis adustus*	X	X	C,P
Spotted hyaena	*Crocuta crocuta*	C,P,S,T	C,P,S,T	C,P,T
Striped hyaena	*Hyaena hyaena*	C,S	X	X
Wild dog	*Lycaon pictus*	S	X	X
Total (including *)		9(10)	11(12)	12(14)

To compare the similarity in carnivore richness (excluding species marked with an asterix) the Sørensen similarity index (1948) was used to calculate a similarity coefficient, defined as:

$$C = \frac{2a}{2a + b + c}$$

where *a* = the number of species held in common, *b* = the number of species unique to the first region and *b* = the number of species unique to the second region (Southwood & Henderson 2000). This showed Loliondo and the Serengeti to be the most dissimilar (*C*=0.70), Ngorongoro and the Serengeti to be the most similar (*C*=0.90) and Loliondo and Ngorongoro to be of in-between similarity (*C*=0.78). However, the high coefficient values between all region comparisons showed a generally high level of species richness similarity between all three study sites.

Sightings diversity during observation-based carnivore index

Table 106 – Carnivore species sighted during logged trips.

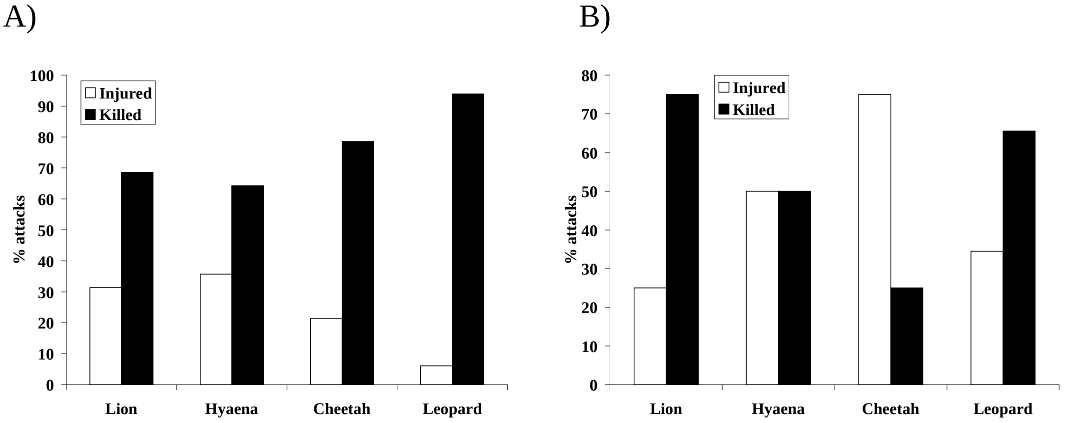
Common name	Latin name	Loliondo	Ngorongoro	Serengeti
Aardwolf	*Proteles cristatus*	N	N	Y
African wildcat	*Felis sylvestris*	N	Y	Y
Bat-eared fox	*Otocyon megalotis*	Y	Y	Y
Black backed jackal	*Canis mesomelas*	Y	Y	Y
Caracal	*Felis caracal*	N	Y	Y
Cheetah	*Acinonyx jubatus*	Y	Y	Y
Golden jackal	*Canis aureus*	Y	Y	Y
Honey badger	*Melivora capensis*	N	Y	Y
Lion	*Panthera leo*	Y	Y	Y

Serval	*Felis serval*	N	Y	Y
Side striped jackal	*Canis adustus*	N	N	Y
Spotted hyaena	*Crocuta crocuta*	Y	Y	Y

10.5 Appendix V – Descriptions of carnivore attacks on livestock

Respondents were asked several questions concerning the details of the attacks described in chapter 6. The results showed that the proportion of lethal attacks differed by species in each Loliondo (χ^2_3=22.4, p<0.001) with cheetah and especially leopard attacks recording a far higher proportion of fatalities. However, Ngorongoro reports did not show significant differences (χ^2_3=5.32, *NS*). Comparisons of individual species showed lion and hyaena attacks were fatal most of the time with no difference between regions (χ^2_1=0.37, *NS* and 1.23, *NS* respectively) but cheetah and leopard attacks were lethal significantly more often in Loliondo than Ngorongoro (χ^2_1=4.0, p<0.05; χ^2_1=14.77, p<0.001)

Figure 65 – Percentage of livestock attacks with lethal consequences in Loliondo (A) and Ngorongoro (B)



Prey choice was compared for each species in each region (Table 107). Lion preference was primarily for adult cattle. However, target species were significantly different in Loliondo and Ngorongoro (χ^2_3=15.1, p<0.05) with Ngorongoro featuring relatively more attacks on sheep and goats. Hyaena targets also differed significantly (χ^2_3=82.7, p<0.001) with attacks in Loliondo more or less equally distributed between adult cattle, calves and donkeys whereas in Ngorongoro more attacks were reported on sheep and goats. All cheetah attacks reported were targeted at sheep and goats whilst the vast majority of leopard attacks were also targeted at sheep and goats with a single report of a calf attack in each region. In general, most attacks involved a single or occasionally two prey individuals. However, two reports in Ngorongoro described

13 cattle and 15 sheep and goats killed in a single night attack by a lion and a single report from Loliondo described a leopard killing 15 sheep and goats.

Table 107 – Percentage prey choice (actual frequency) for every attack described by respondents in Loliondo and Ngorongoro

		Cattle	Calves	Sheep / goats	Donkeys
Lions	Ngorongoro	74 (20)	4 (1)	19 (5)	4 (1)
	Loliondo	90 (81)	4 (4)	1 (1)	4 (4)
Hyaenas	Ngorongoro	16 (3)	5 (1)	42 (7)	37 (8)
	Loliondo	28 (20)	27 (19)	17 (12)	28 (20)
Cheetahs	Ngorongoro	0	0	100 (7)	0
	Loliondo	0	0	100 (15)	0
Leopards	Ngorongoro	0	3 (1)	97 (30)	0
	Loliondo	0	1 (1)	99 (81)	0

Most lion and hyaena attacks occurred during the day (Table 108) with no difference between Loliondo and Ngorongoro (lions: χ^2_1=1.92, *NS*, hyaenas: χ^2_1=0.94, *NS*). All reported cheetah attacks were during daylight hours. Leopard attacks were reported both in the day and at night. The differences between regions were not significantly different (χ^2_1=3.7, *NS*) but most attacks in Loliondo were at night and most in Ngorongoro in the day.

Table 108 - Timing of last reported attack for each species.

		Day	Night
Lions	Ngorongoro	81 (22)	19 (5)
	Loliondo	91 (64)	9 (6)
Hyaenas	Ngorongoro	74 (14)	26 (5)
	Loliondo	61 (35)	39 (22)
Cheetahs	Ngorongoro	100 (7)	0
	Loliondo	100 (7)	0
Leopards	Ngorongoro	35 (11)	65 (20)
	Loliondo	56 (42)	44 (33)

Descriptions of the circumstances of each attack were recorded when given. Most lion attacks occurred on livestock that were grazing under supervision, with a lower percentage occurring at night at the boma and some reported cases of livestock being lost and later found with lions feeding on it. Further details on the methods of attack were gleaned by informal questioning. Lions were described as attacking bomas by scaring cattle by roaring or simply through their presence, causing the cattle to stampede and break out of the boma. Attacks during grazing generally consisted of ambushes. If the herders were capable, they may attempt to drive the lions away. More frequently respondents reported they were alerted of attacks when the children caring for the cattle ran back to the boma, by which time it was too late. There was no difference in frequencies of attack types between regions (χ^2_2=0.02, *NS*). Hyaenas attacked most frequently around the boma or by breaking into the boma at night, but were also blamed for killing a higher proportion of lost animals than lions. Attacks around the boma generally occurred when livestock was returning for the night. Several descriptions mentioned hyaenas attacking stragglers, especially donkeys which are not generally herded like other livestock, or attacking the udders and tails of cattle. There was no significant difference between regions in hyaena attack types (χ^2_3=0.62, *NS*). Most of the attacks attributed to cheetahs occurred whilst livestock were grazing under supervision, with no difference between regions (χ^2_1=0.12, *NS*). Leopard attacks were primarily either raids on bomas, with many respondents describing how leopards could jump in and out of the enclosures whilst carrying a young sheep or goat, or attacks on livestock whilst grazing. Attacks within bomas were reported more frequently in Ngorongoro, but the differences were not significant (χ^2_2=5.9, *NS*).

Table 109 – Attack types

		Inside boma	Outside boma		Found feeding on lost animals
			Grazing	Near boma[1]	
Lions	Ngorongoro	15% (4)	81% (22)	-	4% (1)
	Loliondo	14% (9)	83% (52)	-	3% (2)
Hyaenas	Ngorongoro	29% (2)	0%	57% (4)	14% (1)
	Loliondo	27% (13)	6% (3)	48% (23)	19% (9)
Cheetahs	Ngorongoro	0%	86% (6)	-	14% (1)
	Loliondo	0%	91% (10)	-	9% (1)
Leopards	Ngorongoro	65% (20)	29% (9)	-	6% (2)
	Loliondo	40% (30)	55% (41)	-	5% (4)

[1] Category only used for hyaena attack circumstances

10.6 Appendix VI – Main Maasai interview

Village		Boma name	Date
Name		Boma GPS	Number of gates
Interviewer name	Are others present?	Age	Age set

	Men	Women	Children
Number in *olmarei*			

	Cattle	Shots	Donkeys	No. dogs in boma?	Do you ever grow crops?
Livestock owned					

Please tell me all of the wild animals that live in this area that you can think of:

1	2	3	4	5
6	7	8	9	10
11	12	13	14	15

Can you sort these pictures into animals that are a big problem, small problem or no problem to your village? (*show pictures*)

Big problem	Small problem	No problem
Why?		

Can you tell me the names of these animals in Maa and tell me what you know about them? (*show pictures*)

	Carnivore	Kimaasai word	1st mentioned	2nd mentioned	3rd mentioned	Other
6a)	Lion					
6b)	Hyaena					
6c)	Leopard					
6d)	Cheetah					
6e)	Wild dog					

Can you tell me the difference between…? (*show pictures of leopard and cheetah*)

Differences:

*** EXPLAIN THE DIFFERENCE BETWEEN THE CHEETAH AND THE LEOPARD***

3a) How many cattle/ shoats have you gained over the past month?

	Born	Bought	Gifts	Other
3b) Cattle				
3c) Shoats				

3d) How many cattle / shoats have you lost over the past month?

	Sold	Died	Slaughtered	Given away	Stolen	Predators	Other (list)
3e) Cattle							
3f) Shoats							

4a) Where do you usually graze your cattle?

Cattle		Shots	
Wet season	Dry season	Wet season	Dry season

4b) Who usually looks after the cattle? ____

	Lion	Hyaena	Cheetah	Leopard	Wild dog
When did you last see…? Season? Where? Time of day? How many? Male / females? What were you doing? What happened to the predator?					
Have numbers of…increased or decreased since you were *murra*n?					
When was the last attack on your livestock by…? Season? Where? Time of day? Livestock type? Injured / killed? Who was with the livestock? Adults present? Did they see the attack? Number / sex / ages of predators? What happened to the predator?					
Have attacks by…increased or decreased since you were a *murran*?					
Has anyone in your boma been attacked by ...? Name? Age when attacked? Where attacked (place)? When? Season? What was person doing? Injury? What happened to the predator?					
Have attacks by… on people increased or decreased since you were a *murran*?					

		Yes	No
10a)	Do people in this boma ever need to use poison or traps to control the predators?	How often?	Why not?
10b)	How many lion hunts have you been on?		
10c)	How many lions did your age set kill?		

	What kinds?	How many?
Have you ever killed a predator yourself? (if answer = "no" ask "has anyone else in this boma ever killed a predator?")		

	Yes/No	Why / why not	What kinds?	How often?	Using what weapon?
Do you ever hunt any other kinds of animal?					
Does anyone in this boma ever hunt other kinds of animals?					

What do you think about having wild animals around your village?	
Would you like somebody to come and control some of the wild animals?	
What do you think of the Serengeti National Park and Ngorongoro Conservation Area?	